Solnhofen

A study in Mesozoic palaeontology

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Contents

Contents

vi

Preface

Sedimentary rocks usually teem with fossils, but palaeontologists have long recognized that as a sample of original life they are grossly inadequate. This is simply because in most circumstances only the resistant shells and bones can survive to fossilize. Very occasionally, however, the curtain of preservation is lifted slightly higher and we begin to obtain a glimpse into the extraordinary nature of former life. Such deposits, where delicate and soft-bodied creatures are fossilized, are generally known as fossil lagerstätten. Of these the Solnhofen limestone is the most renowned Jurassic example. Over the centuries this deposit has produced a diverse collection of superbly preserved fossils, including some animals showing soft-part preservation. The Solnhofen organisms are thought to have been washed into hypersaline lagoonal basins and buried rapidly by fine micritic mud, by which means they have been exceptionally preserved.

This book commences with a short history of the scientific and commercial exploration and exploitation of the limestone. The following chapter then puts the Solnhofen limestone into the context of south German stratigraphy and geological history. It next focuses upon events in Late Jurassic times and the Solnhofen area. The third chapter presents a precise petrological description of the Solnhofen limestone from its appearance at outcrop to electron micrographs of the microfacies. Lithological details and geochemical information are used to reconstruct the palaeoenvironment at the site of deposition, and conditions necessary for special preservation. The remaining sections of the book pertain to the fossils themselves: the original palaeoecology of the organisms, the short bursts (or last gasps) of life in the lagoonal basins and the taphonomic processes affecting the fossils from burial until their final exhumation. In the last chapter the fossils are presented taxonomically, accompanied by a striking collection of plates.

Whilst preserving the spirit of Barthel's book, this version is intended for a more advanced readership. It is considerably reordered and more than half is new material. This accommodates a change in emphasis towards discussion of the Solnhofen palaeoenvironment and the conditions required for special preservation. Thus it includes important research material not previously available in an easily accessible form. In particular, emphasis is given to Helmut Keupp's detailed description of the microfacies and discovery of

putative cyanobacterial spheres, together with his resultant stromatolite depositional theory. Meyer & Schmidt-Kaler's excellent book concerning the stratigraphy and palaeobiogeography of the area, published in 1984, has also been an important source of material.

K. Werner Barthel sadly died in 1978, the year after publication of his book *Solnhofen: Ein Blick in die Erdgeschichte*, so that this English edition could not be made with his collaboration. This book was translated and revised by Nicola Swinburne and edited by Simon Conway Morris at the University of Cambridge.

1 The Solnhofen limestone

Introduction: The limestone from Solnhofen

The region known as the Southern Franconian Alb (Südliche Fränkische Alb) lies just to the north of the city of Munich in southern Germany (fig. 1.1). It is a high plateau land whose gently sloping hillsides are cut by a few prominent valleys such as the Danube and the Altmühl. The rivers cut down through many hundreds of metres of Jurassic limestones, and one of these units of limestone,
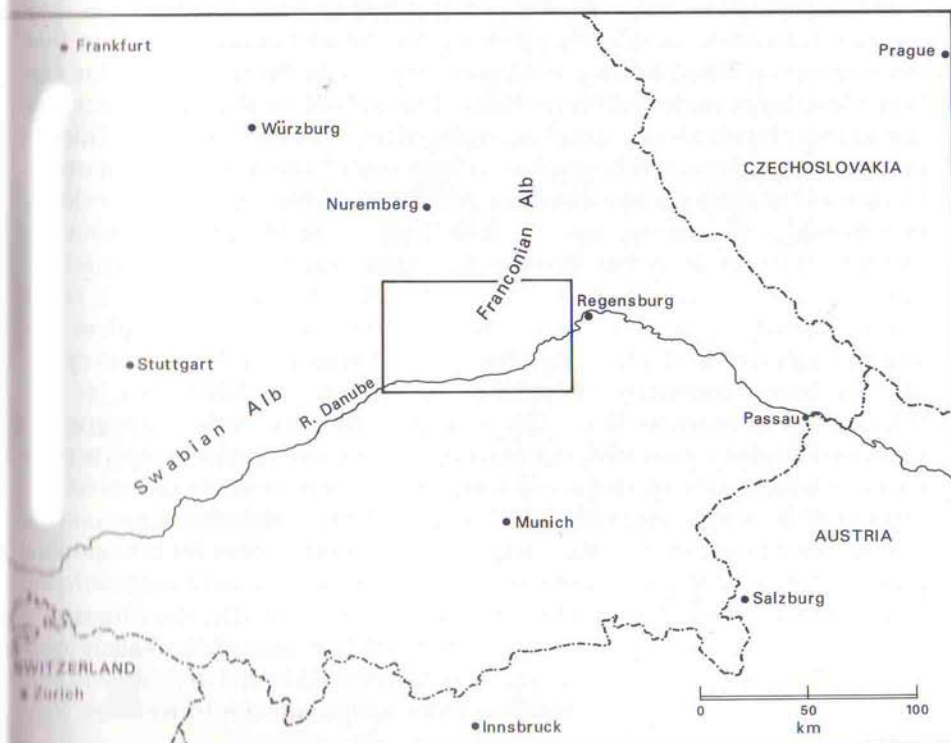
Fig. 1.1 Geography of southern Germany. The boxed area within the Southern Franconian Alb shows the location of fig. 1.2.

that named after the small village of Solnhofen, is known throughout the world for the astonishing richness of its fossils.

To palaeontologists of this century, the Solnhofen limestone is a much acclaimed fossil lagerstätte, a fossil deposit rich in information about life at a certain time (very latest Jurassic) in the earth's past. The quantity of information is large because of the exceptional quality of the specimens, itself a consequence of unique depositional conditions. During deposition, organisms which came to be buried in the Solnhofen mud were likely to be preserved intact, and the Solnhofen fossils are usually complete skeletons, frequently surrounded by an imprint of the original soft tissue. Individually, specimens can present so much detailed information, that the precise relationship of the fossil organism to present-day forms can be established. In the rich assemblage of fossils, in which crinoids, ammonites, fish and crustaceans are numerically most abundant, there are also more fragile forms, such as jellyfish, squids and insects, which normally go unrecorded in the fossil record. But by far the most celebrated fossil is *Archaeopteryx*, whose fame rests on its occupying a crucial taxonomic position between the reptiles and the birds.

In the many collections of Solnhofen fossils the number of specimens may run into thousands, so it is disappointing for the avid collector to learn that (with few exceptions) fossils are actually very rare in this limestone. One can hunt for a day or more and find nothing. The mass of fossils so far collected is due to many hundreds of years of quarrying of the stone, first of all as a building material and then as a lithographic printing stone. The Solnhofen limestone lends itself to these purposes because of its remarkable regularity in bedding (see lithology at outcrop, figs. 3.1 & 3.2, pp. 39 & 40); stacks of laterally continuous layers cleave into flat blocks or thinner sheets. The lithology is best described by adopting the German word of '*Plattenkalk*', but using a small letter (Germans generally use the plural, '*Plattenkalke*'), rather than the vaguer English term of 'platy limestone'. To our mind 'platy' fails to convey the idea of lateral continuity of bedding for distances of kilometres, or the thickness of as much as 30 cm that is reached by some beds. 'Lithographic limestone' is also a poor term in this context as it could restrict comparison to rocks in other parts of the world which have been similarly commercially exploited. It is also inaccurate to describe all the Solnhofen limestone as 'lithographic limestone', as slabs which make suitable stones for lithographic printing are found today only in the quarries of Solnhofen and Langenaltheim where they make up less than 1% of the sequence. Strictly, the lithostratigraphic unit known as the Solnhofen Plattenkalk (i.e. here plattenkalk is used as a proper noun because of its stratigraphic context) is that deposited in the Early Tithonian in the area extending from Langenaltheim to Kelheim (fig. 1.2).

The outcrop of plattenkalk in the Southern Franconian Alb is patchy rather than continuous, with areas of plattenkalk surrounded by more massive,
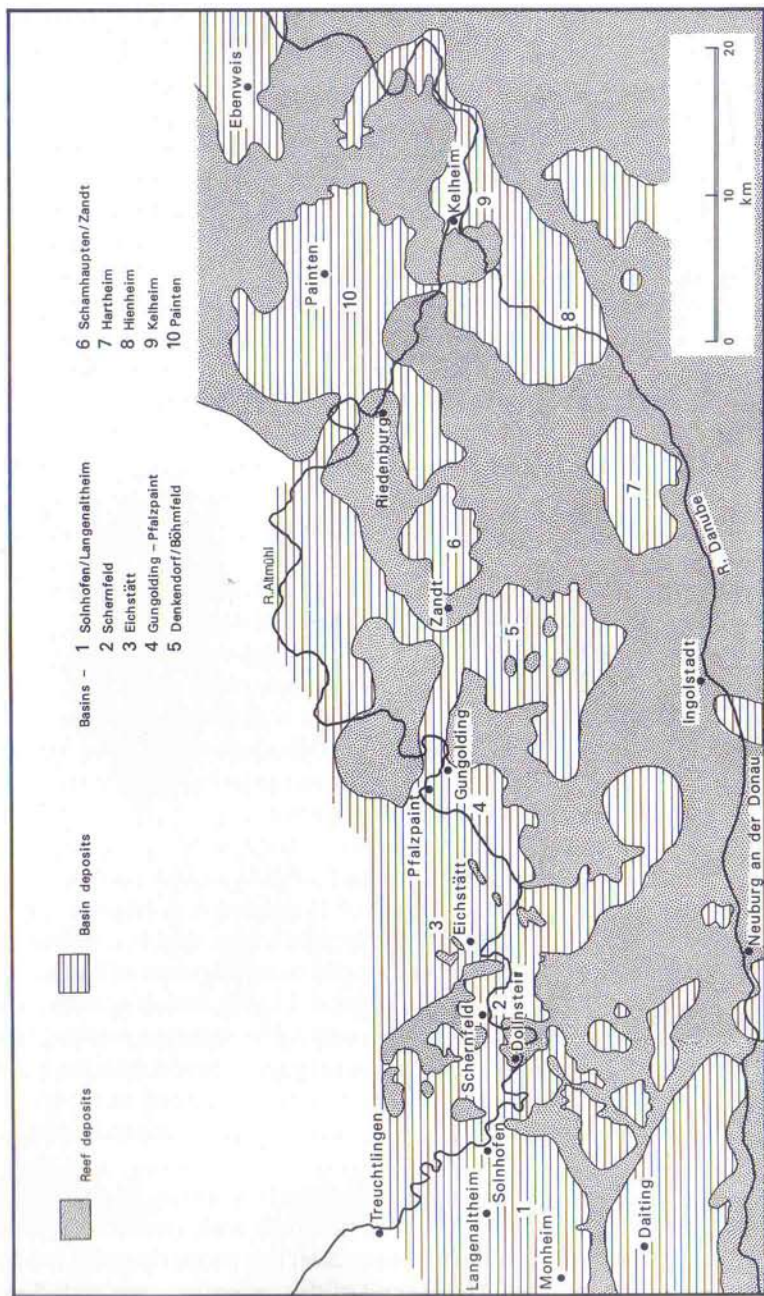
Fig. 1.2   Locality map showing position of the plattenkalk basins amongst the sponge–algal mounds. Updated after Meyer in Meyer & Schmidt-Kaler (1984).

Reef deposits

Basin deposits

Basins –
1 Solnhofen/Langenaltheim
2 Schernfeld
3 Eichstätt
4 Gungolding – Pfalzpaint
5 Denkendorf/Böhmfeld

6 Scharnhaupten/Zandt
7 Hartheim
8 Hienheim
9 Kelheim
10 Painten

biohermal limestones (see fig. 1.2, distribution of plattenkalk basins). The bioherms, mounds of carbonate sediment trapped by growing organisms, projected from the seafloor whilst plattenkalk was deposited in the basins. In each of the basins plattenkalk only forms a part of the total sequence, although most quarries exploit this lithology. Quarries are concentrated in the western part of the area because here the plattenkalk is of the most pure and fine-grained quality. Of these plattenkalks by far the most important is the Solnhofen Plattenkalk. This lithostratigraphic unit varies across the region and rocks from different quarries serve slightly different markets. Quarries to the north of the small town of Eichstätt produce sheets of 1–2 cm thickness which serve as floor and wall tiles, whereas to the east of Eichstätt much thicker slabs are found. Lithographic printing stones come from the area around Solnhofen, where their homogeneous, fine-grained texture and slight porosity make them ideal for this purpose. From the eastern quarries of the Painten area the rock is broken up to make lime.

History of plattenkalk exploitation

Centuries of human culture in the Southern Franconian Alb are expressed in plattenkalk. In the caves of the late Stone Age, plattenkalk was used for scratched drawings and coloured murals. The flat, regular stones of plattenkalk make it ideal as a building material. In Roman times plattenkalk was used in the construction of frontier forts along a defensive wall which stretched across the plattenkalk area and kept out the northern Germanic tribes. The Romans also used the stone as a facing stone, for example in the lining of baths (fig. 1.3), and plattenkalk tablets were also used for inscriptions.

In the Middle Ages the stone continued to be used in the construction of houses and other buildings, especially for floor (fig. 1.4) and for roof covering. It was also a valuable export. In the church of Hagia Sofia in Istanbul can be found a medieval mosaic floor made from plattenkalk tiles, which, according to a thirteenth-century chronographer were shipped from the town of Kelheim in the Southern Franconian Alb. The architectural flourish which accompanied the Renaissance era of the sixteenth and seventeenth centuries profited from the use of plattenkalk. Mansions and cottages alike were paved with the highly prized stone. Sculptors scraped and chiselled the fine-grained material into gravestones and memorial plaques (fig. 1.5), some of which are still visible in local churches today.

Another method of producing a relief employed by artists of this period involved the etching of uncovered portions of the stone with a weak acid. It was Alois Senefelder in 1793 who was the first to exploit this properly and it led him to the 'discovery' of lithography. The legend of this invention runs as follows: Senefelder wished to make a list of a number of items which he wanted a washer
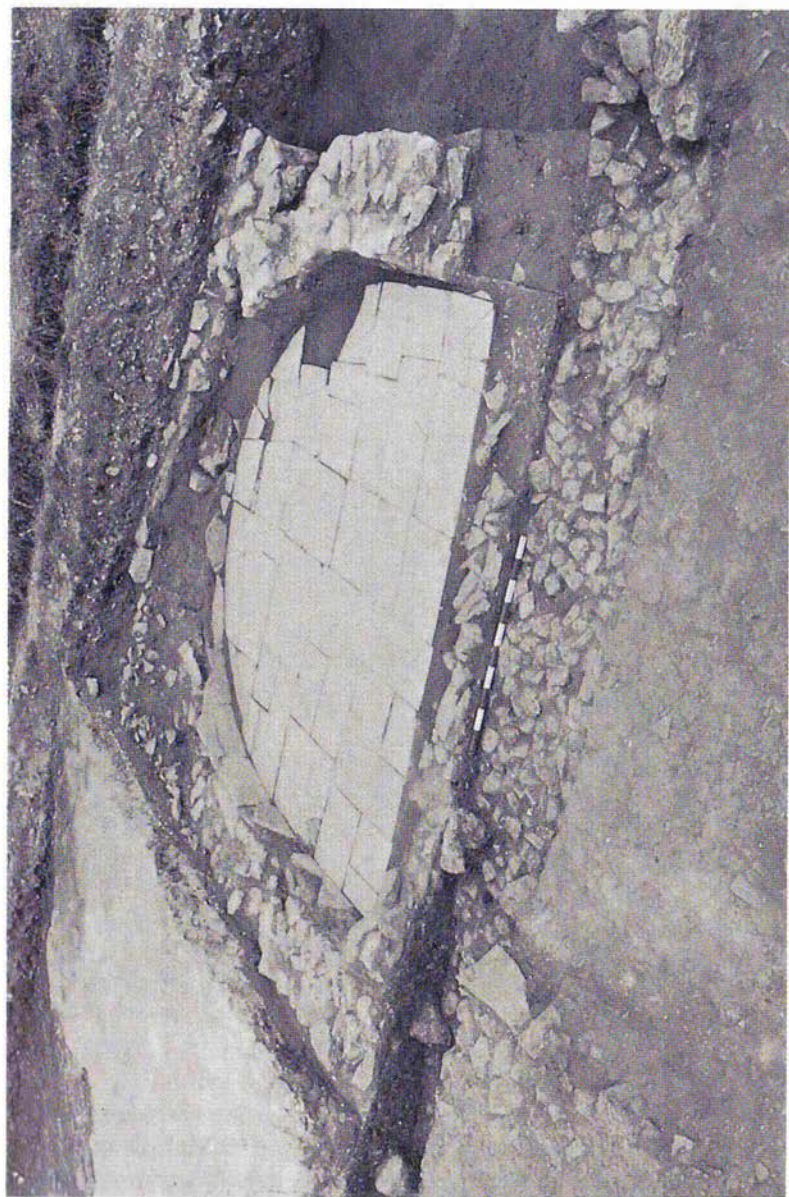
Fig. 1.3   Plattenkalk tiles used in the floor of a Roman bath or 'tepidarium' at the Roman site of Iciniacum, near Theilenhofen, in the Weissenburg area. The bath has now been rebuilt in the Museum of Solnhofen Aktienvereins at Maxberg bei Solnhofen. Scale in the foreground 1 m.

Fig. 1.6 Examples of lithographic plates. The top surface of the lithographic block is finely polished and the design painted on to the block using a fatty lithographic ink. Before printing the block is wetted with water which is absorbed by the unpainted areas of the stone. When the block is inked in the printing process, only those parts which were covered with the lithographic ink will take up the printer's ink, whilst the other parts of the block will repel it. Plates each around 300×250 mm; in the Museum of Solnhofen Aktienvereins, Maxberg bei Solnhofen.

plattenkalk over their heads. More suitable for steeper roofs, is the alternative method whereby tiles with a shaped, semicircular end are laid to form a pattern resembling a beaver's tail (fig. 1.9). Today, modern synthetic tiles are used to an increasing extent and the old tradition is disappearing.

Plattenkalk is still quarried by the same methods that have been used for centuries. The work in extracting and preparing the slabs is almost entirely manual, the only piece of machinery adopted being a digger used to clear away surface debris. From then on everything is done by hand. A sledge-hammer is used to free suitable blocks (fig. 1.10), and a lighter hammer to begin shaping the stones, and in the workshop on site a trimming hammer and a specialized pair of tongs are used to perfect the shape (fig. 1.11). Only about a quarter of the material is suitable as a building stone and of this the poorer quality, but still frost-resistant, slabs are left unshaped for garden paths and terraces. A very small percentage of stones is suitable as lithographic printing stones. These stones are handled with care and finely polished.

Fig. 1.7 Drawing of Senefelder's original lithographic press.
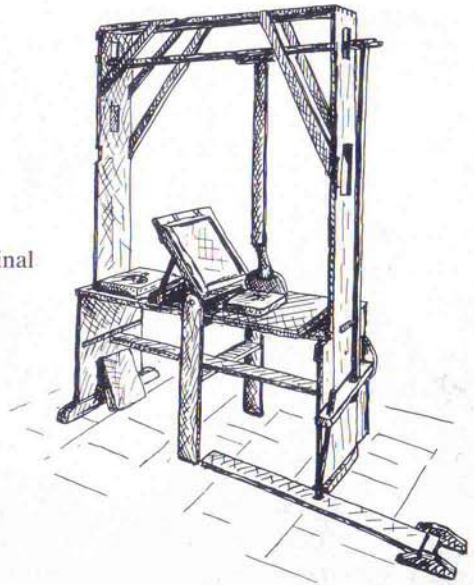
Fig. 1.8 A traditional method of tiling using thin, unshaped plattenkalk tiles (known as a *'Legschiefer'* roof). This method is suitable only for covering flat roofs.
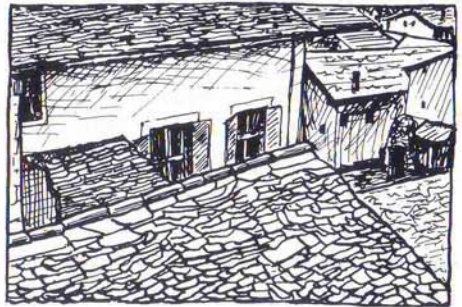
Collections of fossils

Man discovered fossils in the Solnhofen rocks long ago. In the late Stone Age they are known to have been guarded as ornaments or perhaps used as amulets designated with magical properties. Fossils have always been much prized by the locals for their beauty. Naturally most fossils were found by the men who quarried the stone as a building material. At first quarry owners allowed the men to keep the fossils and so quarrymen built collections. As the fossils became well known, so quite a trade developed with buyers from both home and abroad. The inflation in price was noted as early as 1781 by J. B. Fischer, who reported: 'In recent times the price of these rarities has soared and it is not
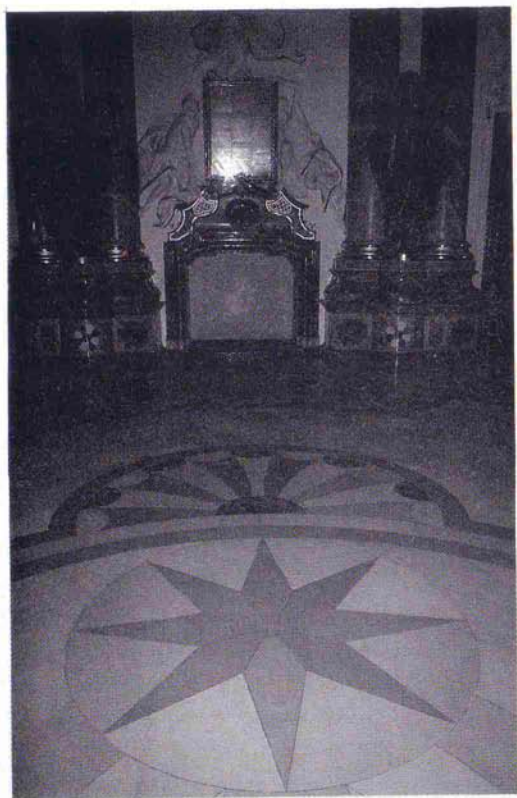
Fig. 1.4 Mosaic floor made of plattenkalk, in the Abbey of Otto-beuron, Bavaria, exemplifying the subtle variations of shade in this decorative stone. Photo by Rolf Wihr, Bamberg.

woman to collect. As he had no paper to hand, he began to write on a slab of limestone and used a rather greasy ink. To make the message more prominent he washed the slab with a weak acid which was only absorbed by those parts of the limestone not covered with the ink. This had the effect of dissolving away the surrounding limestone and enhancing the letters from the background. When a sheet of paper was placed on the stone he produced an exact mirror-image print of the inked design on the stone. Senefelder immediately recognized the possibilities and spent some time perfecting the art. The precise replication of a drawing by this method has ensured its popularity with artists of many generations. Some of the most memorable examples of this art come in the grand lithographic plates of Henri Toulouse-Lautrec, the sharp images with which Honoré Daumier portrayed the weaknesses of his fellow men, and the drawings by which Käthe Kollwitz emphasized human suffering. Some examples of lithographic plates together with a lithographic printing press are presented in figs. 1.6 & 1.7.

The heyday of lithography was to last a mere hundred years, after which it was surpassed by newer and cheaper processes. Today few lithographic stones
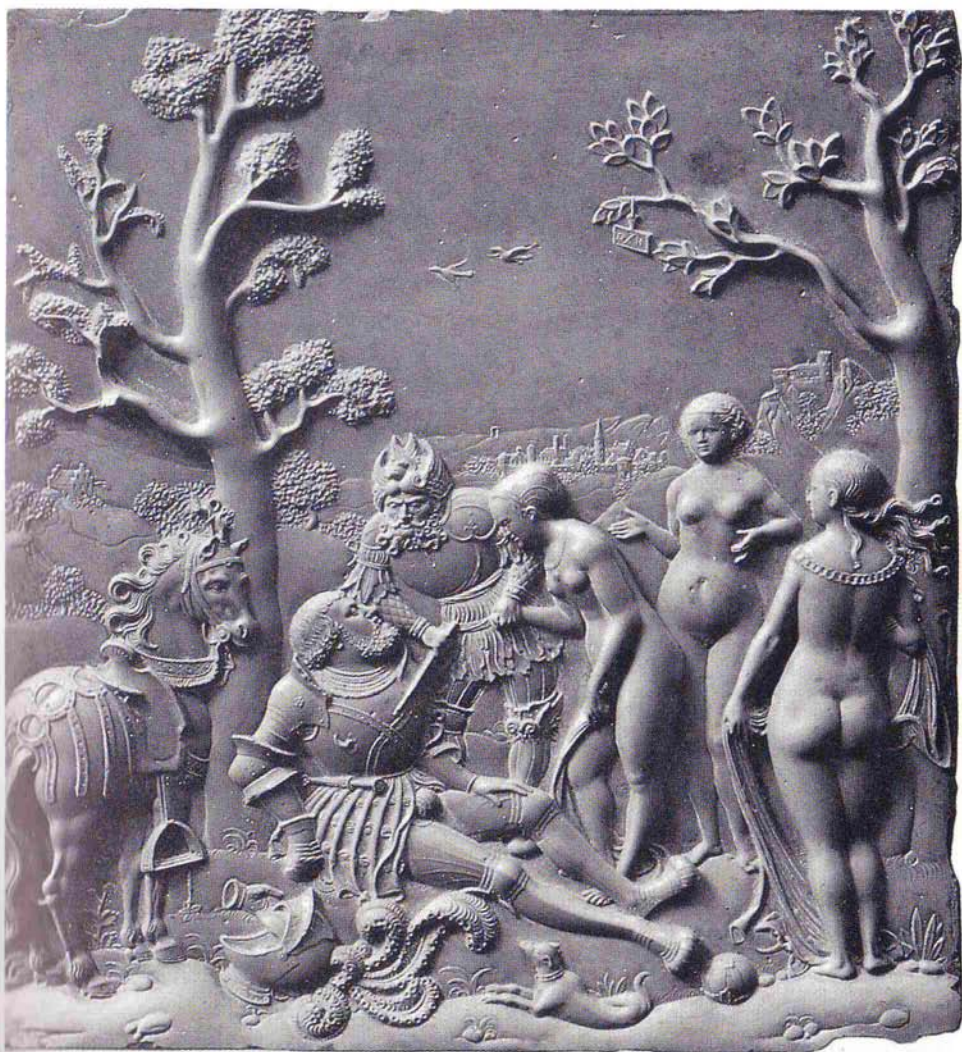
Fig. 1.5 Bas-relief in Solnhofen stone entitled 'The judgement of Paris' by Doman Herring, copied from an original woodcut by Lucas Cranach in 1508. Now in the sculpture section of the State Museum in Berlin. Size 220 × 197 mm.

are required and plattenkalk is mainly quarried for use as a building material, both for local needs and for export. Shaped and polished tiles make fine floor and staircase coverings and window surrounds. Roofs of Solnhofen slate give the local houses a distinct charm. The older and poorer houses have flattish roofs and a thick covering of thin and unshaped tiles (fig. 1.8). When the roof has to be repaired new tiles are lain over the old and broken ones so that in some of the oldest houses people may have up to half a metre thick of

Fig. 1.9   Roof made of shaped tiles of Solnhofen Plattenkalk (known as a '*Zwicktaschen*' roof). This is typical of older buildings of the Altmühl area. Photo by N. H. M. Swinburne.

unusual to find that a fine, well preserved piece with both the concave and convex sides would fetch one, two or perhaps even four ducats' (from Schwertschlager in 1919).

One of the first major scientific concerns with the Solnhofen fossils is demonstrated in the description published in Latin by J. J. Baier in 1708. The full title of this work is *Oryktographia Norica sive rerum fossilium et ad minerale regnum pertinentium in territorio Norimbergensi ejusque vicinia observatarum succincta descriptio*, in effect, 'A description of fossils from the Nuremberg region'. With the resurgence of interest in the natural sciences at the beginning of the nineteenth century and the increased popularity of palaeontology came the first systematic collections and detailed publications. Amongst the first important monographs about the Solnhofen flora and fauna are those of E. F. Germar, A. Hagen, Graf Georg zu Münster, Albert Oppel, Baron Friedrich von Schlotheim and Andreas Wagner, whose names are preserved for posterity in the fossils they described. The basis for much of the current knowledge of reptiles stems from the numerous works of Hermann von Meyer, and this scientist has also gone down in history as the author of the original description of *Archaeopteryx*.

In 1860 an isolated feather was found in the Solnhofen rocks (fig. 7.96). This

Fig. 1.10 Splitting the plattenkalk slabs. Piles of slabs break free from the rock along natural vertical joints and they are then split along bedding planes. All work is manual taking place outdoors in summertime, and under make-shift roofs in wintertime. Only about half the stone can be used and the rest is thrown on the spoil tips.

unexpected discovery of bird remains in rocks which dated from the age of the dinosaurs caused a sensation. (The find did not however extend the stratigraphic range of the birds; the tracks of some bipedal dinosaurs, misinterpreted as bird footprints, were already known from the Triassic.) A year afterwards the skeleton of a feathered creature was unearthed. When examined closely the skeleton was clearly that of a reptile, but was surrounded by the unmistakable imprint of feathers which impelled its classification as a bird. The first *Archaeopteryx* was obtained by a local doctor, Carl Häberlein, who collected fossils. Häberlein actually received *Archaeopteryx* from one of his patients in lieu of medical expenses. With the great importance attached to this specimen a price of £700, considered exorbitant at the time, was extracted from the British Museum (a price which included a large number of other Solnhofen fossils) and the first *Archaeopteryx* came to reside in London.

The find could scarcely have been made at a more opportune time. Only two years earlier Darwin had published his first edition of *On the Origin of Species* and *Archaeopteryx* (ancient wing) was hailed by some as Darwin's predicted 'missing link' between the reptiles and the birds. It is surprising that Darwin's
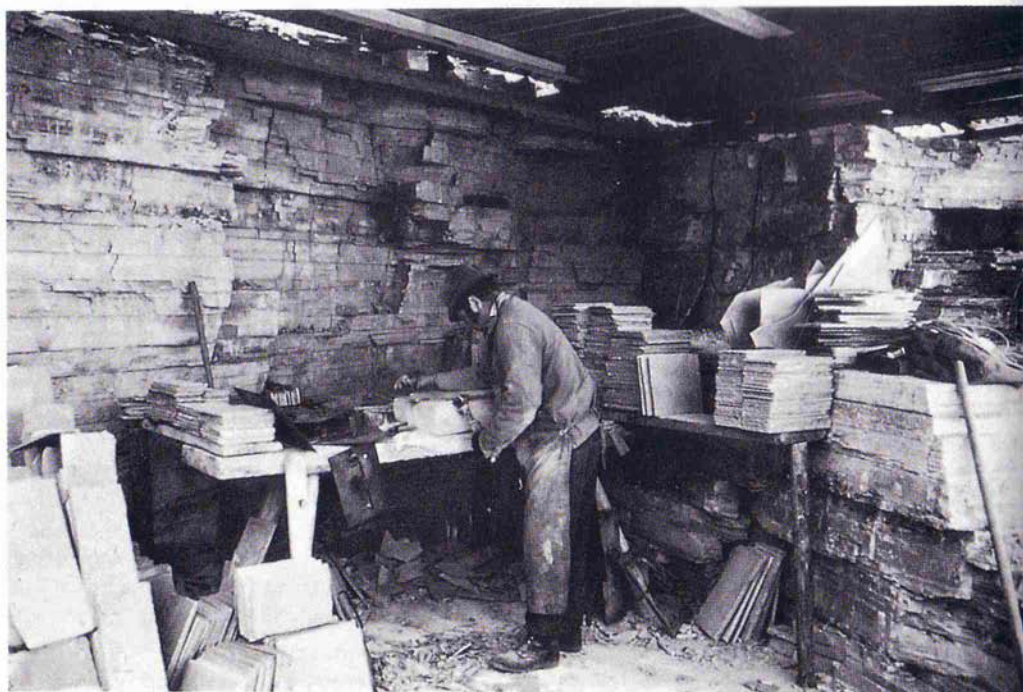
Fig. 1.11 Shaping and trimming in the workshop. In the workshop the slabs are trimmed with a special hammer and tongs. This picture shows the thin flinz beds which will be used mostly as decorative tiles for floors, walls and window sills.

strongest advocate, T. H. Huxley, did not, at first, see *Archaeopteryx* as a form transitional between the reptiles and the birds but as a fully fledged bird. Huxley had thought that the birds had evolved from small running dinosaurs (a view with which we now agree), although via flightless birds similar to ostriches, and as long ago as the Palaeozoic. Huxley used the small Solnhofen dinosaur *Compsognathus* (which was known from the one specimen described by Wagner in 1861) as an example of a bird-like reptile and later remarked on its similarity to *Archaeopteryx*, the reptile-like bird. *Archaeopteryx* was formally described by the British palaeontologist Richard Owen who, although he believed evolution had taken place, was vigorously opposed to Darwin's theory of Natural Selection. By profession a comparative anatomist, he believed that the variety of life could be explained as predetermined modifications on a general plan and had constructed notions of what he believed to be an 'archaetypal vertebrate'. His interest in *Archaeopteryx* focused more on the supposed presence of embryonic characteristics, such as the unfused vertebrae in the tail, that revealed the nature of the archetype. Although *Archaeopteryx* was, for him, clearly a bird he did see it as a 'transitional form', although he

thought that *Archaeopteryx* had evolved from the long-tailed pterosaur *Rhamphorhynchus* (see Gould 1987).

Nowadays we think that small running dinosaurs, relatives of *Compsognathus*, could have given rise to *Archaeopteryx* some time in the Late Jurassic. Both *Archaeopteryx* and *Compsognathus* are described in chapter 7, where the reader can see just how similar the creatures are. The evolution of *Archaeopteryx*, the acquisition of feathers and the origin of flight are subjects still being actively debated. (The reader is referred to the symposium volume of the *Archaeopteryx* conference, held in Eichstätt, in 1984, edited by Hecht *et al.* 1985.)

Recently, *Archaeopteryx* has again been in the public eye because of allegations by the physicist Fred Hoyle and mathematician Chandra Wickramasinghe (1986) that the fossils are the result of clever nineteenth-century forgeries. They claim that skeletons of the small dinosaur *Compsognathus* were taken, areas around the bones excavated and then infilled by a paste made of ground-up limestone together with a binding agent. The feathers of a modern bird were then pressed into the cement to make the impressions around the skeleton. Hoyle and Wickramasinghe claim a major conspiracy involving Häberlein, Owen (who allegedly commissioned the forgery in order to undermine Darwin and Huxley) and a succession of curators at the Natural History Museum. Hoyle and Wickramasinghe's allegations have been shown elsewhere (Charig *et al.* 1986, Swinburne 1988, amongst others) to be mischievous and utterly without foundation.

In 1877 a second *Archaeopteryx* was found. It possessed even finer features as well as a complete skull and was sold to the museum of Berlin by Dr Häberlein's son, Ernst Häberlein. This Häberlein, together with another doctor, Dr Redenbacher from the local town of Pappenheim, assembled a fine collection of Solnhofen fossils in the middle of the nineteenth century. Specimens in many museums still bear the labels saying 'Haeberlein'sche Sammlung' (from Häberlein's collection) or 'Redenbachersche Sammlung'.

Archaeopteryx was but one of the splendid fossils from the Solnhofen localities and interest in the entire range of fossils was stimulated. Major collections were established and these encouraged a consideration of the Solnhofen fauna and flora as a whole. The first list of fossils was compiled by Ludwig Frischmann in 1853. In 1904 Johannes Walther published a comprehensive work entitled *Die Fauna der Solnhofener Plattenkalke*. This summarized Frischmann's list into a total of 650 known species, now thought to be an over-estimate as it includes many incomplete and juvenile specimens as separate species. A more accurate figure is thought to be around 600 (G. Viohl, pers. comm. 1986). Walther was also first to deal with the relationship of the organisms to the sediment in which they were buried. In particular he observed that almost all specimens were located on the underside of limestone blocks. Walther proposed that the limestone was deposited in a lagoon bordered by

land to the south and with a barrier reef and the open sea to the north. Marine sediment was carried over a barrier reef into the lagoon where it settled, the water then drained back to the sea, through the reef, leaving a sticky mud. The clayey interbeds were dilutions of this marine lime mud by terrestrial dust. Today the main tenets of this theory still remain although the situation of land and sea is approximately reversed (see fig. 4.1, p. 57), and there is no need to postulate a period of subaerial exposure for the sediment (see deposition, p. 56).

In the present century we have come to know much more about carbonate sedimentology, but our knowledge of the fossils has, in some cases, scarcely progressed. Some groups have not been reconsidered since their original nineteenth-century descriptions although other fossils, such as the reptiles and of course *Archaeopteryx*, have received much greater attention. After the first two skeletons of *Archaeopteryx* were found in the late nineteenth century it took another hundred years until four more were recovered. *Archaeopteryx* no. 3, of which only the torso is present, was found in 1956 at Langenaltheim, the same locality as the first bird, by a quarry worker in whose possession it still remains. It was described in 1959 by Florian Heller. The next two were, curiously enough, already lying in museums. The *Archaeopteryx* which came to light in 1970 had actually been dug up in 1855, some five years before the discovery of the first feather. This bird had lain in a museum in Haarlem in Holland under the title of the small flying reptile '*Pterodactylus crassipes*', to which it is superficially similar. On closer examination the imprints of feathers around the body were observed, meriting its reclassification as *Archaeopteryx*, and it has since been described by John Ostrom (1970). The fifth individual is the famous Eichstätt specimen. It is complete, although about two-thirds the size of the others and differs in other important respects. Found in 1951, it was provisionally described only in 1973, but has subsequently been monographed by Peter Wellnhofer. It is on public display at the Jura-Museum in Eichstätt.

Very recently, a further, sixth specimen has been recognized. This specimen, which was also collected several years ago, was found by a Turkish migrant who worked at one of the Solnhofen quarries. He sold the fossil to one of the larger Solnhofen collections, that belonging to the community of Solnhofen, the Bürgermeister-Müller-Museum, where it is now on display. He claimed that the fossil came from the Solnhofen region, although it should then have belonged to the quarry owners and he could not have rightfully sold it. However, the slab in which the fossil lies is of the type much more typical of the Eichstätt area. Once in the museum it lay undisturbed until the curator, Herr Müller, came across it, cleaned and prepared it, and came to the conclusion that it was the small dinosaur *Compsognathus*. As this in itself would have been quite noteworthy, Müller showed it to the curator of the Jura-Museum, Eichstätt, Günter Viohl. Viohl noticed that the arms were too long compared with the length of the body for it to be *Compsognathus*, and that there were the

impressions of feather veins under the left wing. The specimen is now accepted as the sixth example of *Archaeopteryx* and (despite its dubious origin) is known as the Solnhofen specimen. Details of this latest find, together with all other examples of *Archaeopteryx* are listed in Table 1.1.

Table 1.1 The *Archaeopteryx* specimens

Name	Year of find	Original locality	Description	Present housing
Feather (part and counter-part)	1860	Solnhofen	H. v. Meyer 1861	(a) East Berlin, Museum für Natur-kunde der Humboldt-Universität (b) Munich, Bayerische Staats-sammlung für Paläontologie und historische Geologie
1st, or London specimen	1861	Langenaltheim (Solnhofen)	H. v. Meyer 1861 (announcement of find) R. Owen 1863 (full description)	London, British Museum (Natural History)
2nd, or Berlin specimen	1877	Blumenberg, Eichstätt	W. Dames 1884	East Berlin, Museum für Natur-kunde der Humboldt-Universität
3rd, or Maxberg specimen	1956	Langenaltheim (Solnhofen)	F. Heller 1959	Solnhofen, private ownership
4th, Haarlem or Teyler specimen	1855	Riedenburg	H. v. Meyer 1875 (as a pterosaur) J. H. Ostrom 1970 (as *Archaeopteryx*)	Haarlem, Teyler Museum
5th, or Eichstätt specimen	1951	Workerszell, Eichstätt	F. X. Mayr 1973 (provisional de-scription) P. Wellnhofer 1974 (full descrip-tion)	Eichstätt, Jura-Museum
6th, or Solnho-fen specimen	1960s	Eichstätt area	P. Wellnhofer 1988a (provisional description) P. Wellnhofer 1988b (full de-scription)	Solnhofen, Bürgermeister-Müller-Museum

Today, the world-wide acclaim for the Solnhofen fossils has ensured that important fossils are either incorporated into the collections of the quarry owners or find their way into the hands of dealers. To acquire a decent specimen of, say, a pterosaur would involve thousands of deutschmarks and an *Archaeopteryx* would be almost unpriceable! As fossils may even be an important part of the economy of the quarry, the working quarries exclude fossil hunters. There are various disused quarries, but fresh rock is covered by debris piles which have been thoroughly scoured for fossils over the centuries. However, a few quarries have been especially designated as fossil quarries and here fresh sections are accessible and may be worked by amateurs. Although it is certainly less easy to come across fossils by accident than it once was this does not seem to have affected the popularity of fossil hunting. In fact, this activity is so popular that entire German families will come to the region on fossil collecting holidays.

For visitors to the area the magnificently situated Jura-Museum in Willibaldsburg, Eichstätt, houses the largest of the public collections. Also in the Eichstätt area, at Harthof, is the private collection of the Museum Bergér. In Solnhofen itself is the Bürgermeister-Müller-Museum as well as a large private collection open to the public at the Maxberg Quarry (Museum des Solnhofen Aktienvereins). The Bavarian State Museum (Bayerische Staatssammlung für Paläontologie und historische Geologie) in Munich is also well worth a visit.

2 Geological history and stratigraphy

Geological history of the Southern Franconian Alb

The stratigraphy of Bavaria in southern Germany is relatively simple. The bedding dips gently towards the southeast causing Jurassic rocks to outcrop over most of the Southern Franconian Alb (figs. 2.1–2.5). To the north and northwest these pass downwards into Triassic sediments, whilst to the south and southeast they are overlain by deposits laid down in the Tertiary Period.

The older Palaeozoic rocks, which are metamorphosed and riddled with igneous intrusions, underlie the area, but in the east are brought to the surface in the fault blocks of the Bohemian Massif. In Palaeozoic times these rocks formed parts of a series of ancient mountain ranges which ran east–west across southern Germany. These mountains were formed during a tectonic episode known as the Hercynian (Variscan) orogeny which culminated late in the Carboniferous Period at around 300 Ma. The mountains were subject to erosion so that by the beginning of the succeeding Permian Period they had been worn down to expose their metamorphic and granite core. In the following periods these harder rocks persisted as a topographic high, known as the Vindelicisch Land, the position of which dominated regional palaeogeography until the end of the middle part of the Jurassic Period (see fig 2.6). Through time the Vindelicisch Land subsided and began to be covered by sediments. In Early Permian times continental sediments accumulated in the initial depressions. Thereafter, as the land sank, the sea gradually transgressed southeastwards. To the northwest of the Southern Franconian Alb marine sediments, such as the well-known Middle Triassic Muschelkalk, were deposited, enclosing fossils such as ceratite ammonoids and oysters. In contrast, Triassic sediments of the Southern Franconian Alb are mostly non-marine shales and sandstones, laid down in fluviatile and deltaic settings.

Fully marine deposition over the entire area did not begin until the Jurassic Period when the Southern Franconian Alb lay under the shallow waters of a wide shelf sea. Sediments of Early Jurassic age (Lias) are dark shales and argillaceous (clayey) limestones and the period is often referred to as the Black Jurassic. In the succeeding middle part of the Jurassic (Dogger) Period sandstones predominate, and this interval is often called the Brown Jurassic. As the sea advanced during Middle Jurassic times, the coastline migrated to the
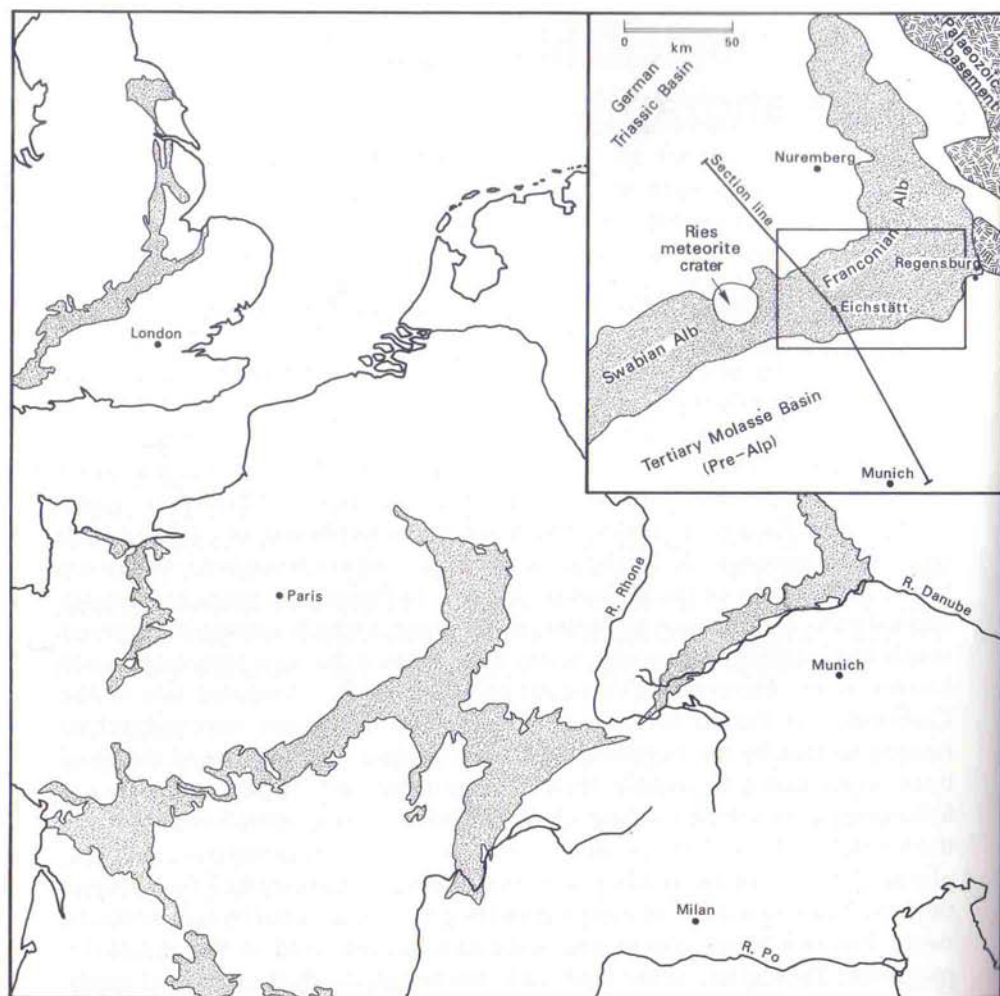
Fig. 2.1 Outcrops of Jurassic rocks (stippled) in northern Europe. The inset shows the situation in the Southern Franconian Alb and the section line of fig. 2.2. Adapted from Meyer, in Meyer & Schmidt-Kaler (1984) and Viohl (1985).

south and east but the palaeogeography was complicated by the development of a northwesterly projecting spur of resistant land around Landshut with a corresponding indentation known as the Regensburg embayment. Continued incision of the Regensburg embayment into the coastline eventually breached the Vindelicisch Land barrier. The northern waters became connected to the southerly Tethys Ocean and the Vindelicisch Land became an island.

So it was that by Late Jurassic (Malm) times, where the rocks are often called the White Jurassic because of the abundance of limestones, the continuing
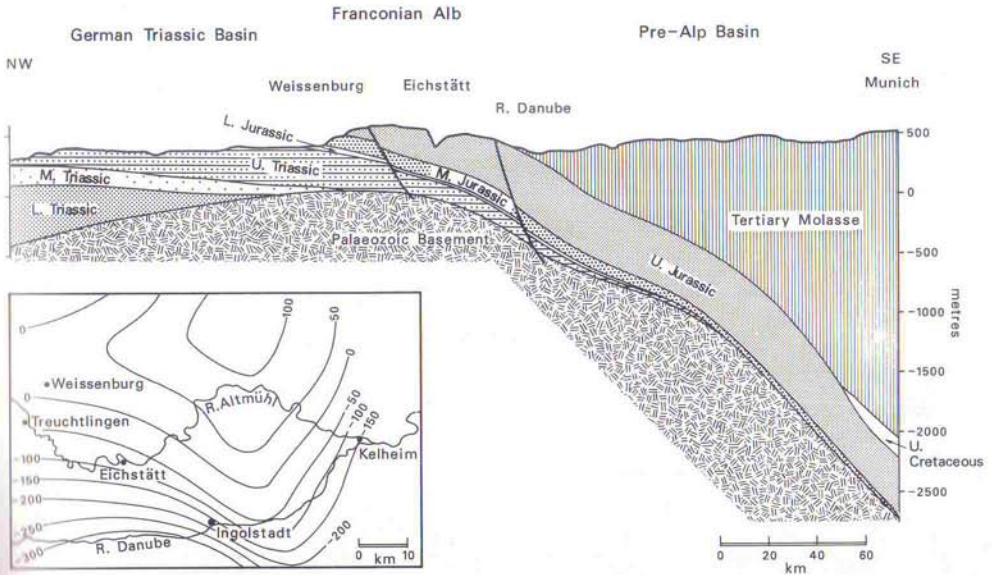
Fig. 2.2. Generalized geological section through strata of the Southern Franconian Alb, with map showing depth in metres to the Palaeozoic basement. Adapted from Meyer & Schmidt-Kaler (1984).

marine transgression had completely flooded the Vindelicisch Land. The influence of land now came from the north from the uprising 'Mitteldeutsche Schwelle'. For the first time the Southern Franconian Alb could exchange waters directly with the Tethys Ocean. However, evidence from recently drilled boreholes to the south of Munich (used in the palaeogeographic reconstruction of Meyer, see fig. 4.1, p. 57) suggests that such an interchange of waters would have been impeded by carbonate shoals which lay under only a few metres of water on the northernmost margin of Tethys. In this tranquil setting organically mediated carbonate mounds and reefs spread across the carbonate platform of the Southern Franconian Alb. Between the reefs lay small basins which were infilled by light coloured limestones and argillaceous limestones. These included the Solnhofen Plattenkalk.

Towards the very end of the Jurassic, deposition over the Southern Franconian Alb came to an end, as land emerged in the northwest and east and the Tethys sea regressed to the south. Exposed until Upper Cretaceous times, the Mesozoic sediments were then subjected to the actions of wind and weather. Thereafter, there was only one, short further period of widespread marine sedimentation which took place at the beginning of the Upper Cretaceous (in the Cenomanian–Turonian stages, around 95 Ma). The sea advanced from the southeast, flooding the area from Ries to Regensburg and laying down sandstones and impure limestones. Around Regensburg this sediment is now

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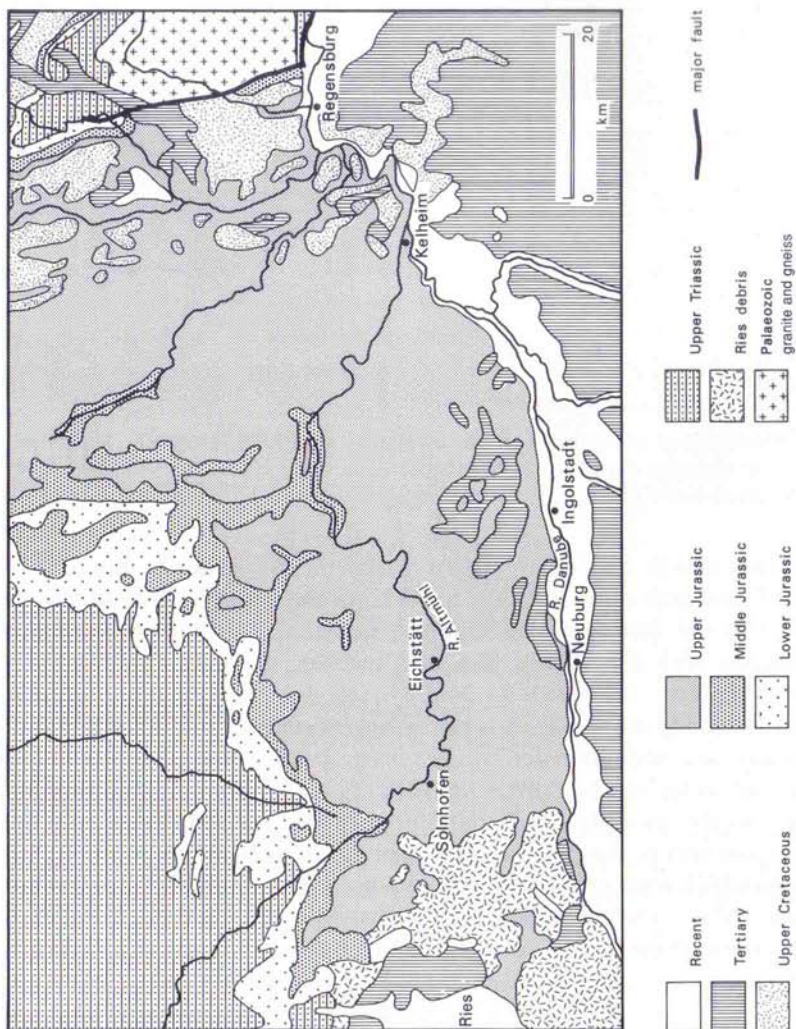
Fig. 2.3 Geological map of the Solnhofen area. The Mesozoic strata dip gently towards the SSE. Older rocks outcrop in fault blocks in the east of the area.

Recent

Tertiary

Upper Cretaceous

Upper Jurassic

Middle Jurassic

Lower Jurassic

Upper Triassic

Ries debris

Palaeozoic granite and gneiss

major fault

Regensburg

Kelheim

Eichstätt

Solnhofen

R. Altmühl

R. Danube

Ingolstadt

Neuburg

Ries

0   km   20

		STAGE	Quenstedt's Subdivision of Swabian Jurassic	Conventional Subdivision
UPPER JURASSIC or MALM		Tithonian	ζ	ti_{1-6}
	Kimmeridgian		ε	ki_3
			δ	ki_2
			γ	ki_1
	Oxfordian		β	ox_2
			α	ox_1

Fig. 2.4 Nomenclature for subdivision of the Jurassic Period.
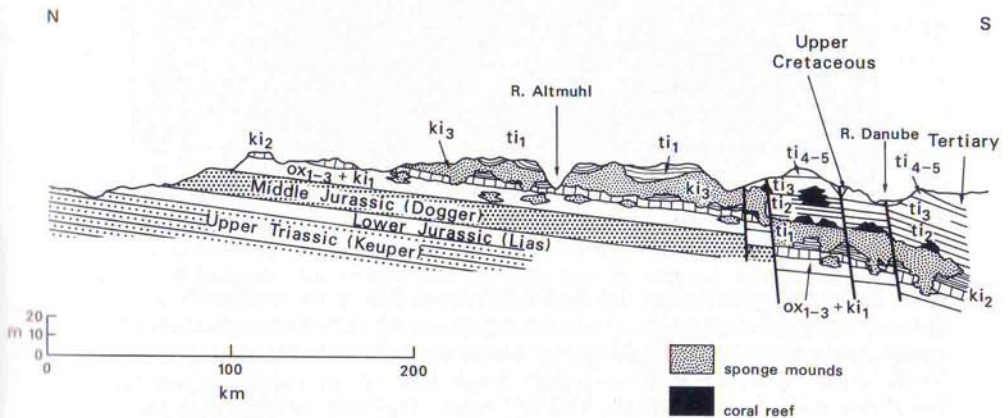
Fig. 2.5 Section through strata of the Solnhofen area. The best exposures occur in river valleys such as those now occupied by the Danube and Altmühl.

exposed, but in the Solnhofen area, where it was once deposited over the plattenkalk, it has since been eroded away. Evidence for its presence remains only in the Neuburg area, in the form of a few silicified knolls, which resisted erosion, and sediments which survived by having been piped or channelled into caves beneath the previous erosion surface.

Since the last retreat of the seas, the Southern Franconian Alb has remained

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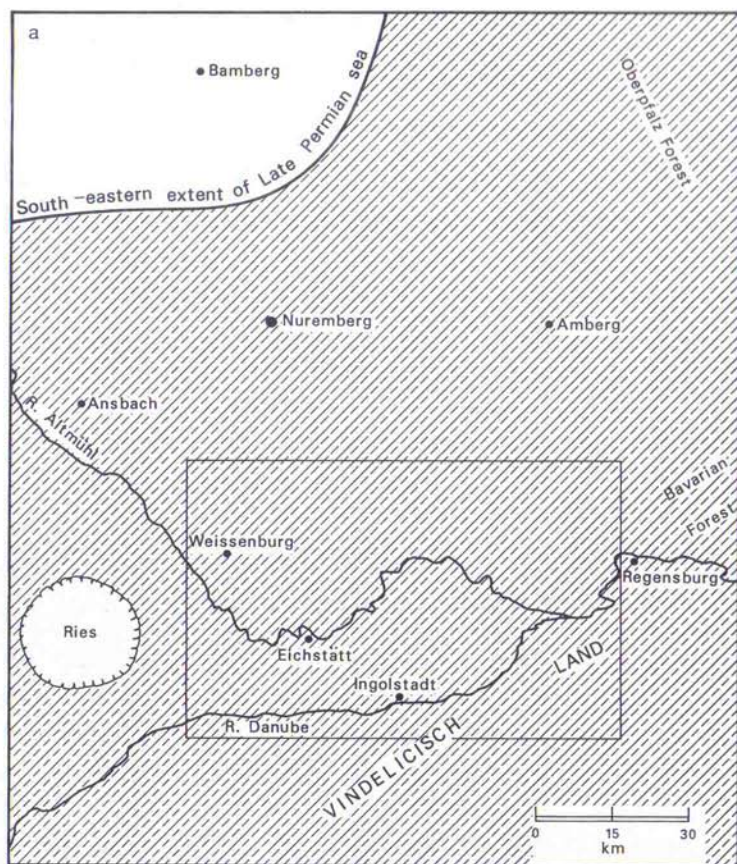
Fig. 2.6 (parts b–d on pp. 23–25) Development of regional palaeogeography from Permian to Jurassic times. This period is marked by a major transgression from the NW. By the end of the Triassic Period the sea had completely flooded the Southern Franconian Alb with the Vindelicisch Land remaining on its southern side. In Early Jurassic times an embayment cut into this landmass, which by Middle Jurassic times had established a connection with the Tethys Ocean further south. In Late Jurassic times the Vindelicisch Land had been completely flooded. Boxed area delimits region around Solnhofen. (a) Late Permian; (b) Middle Triassic; (c) Early Jurassic; (d) Late Jurassic. (Arrows indicate directions of transgression.) Redrawn from Schmidt-Kaler (1979).

exposed to the elements. When earth movements associated with the formation of the Alps caused a sea to spread right across Switzerland and Austria, the coastline lay to the south of the present-day Danube and at this time the Southern Franconian Alb was an important area of sediment supply. A major event in the geological history of the area took place in the Tortonian stage of the Miocene Period (at 15 Ma). At a locality to the west of Solnhofen (Ries), a vast crater 22 km in diameter was created by the impact of a large meteorite.
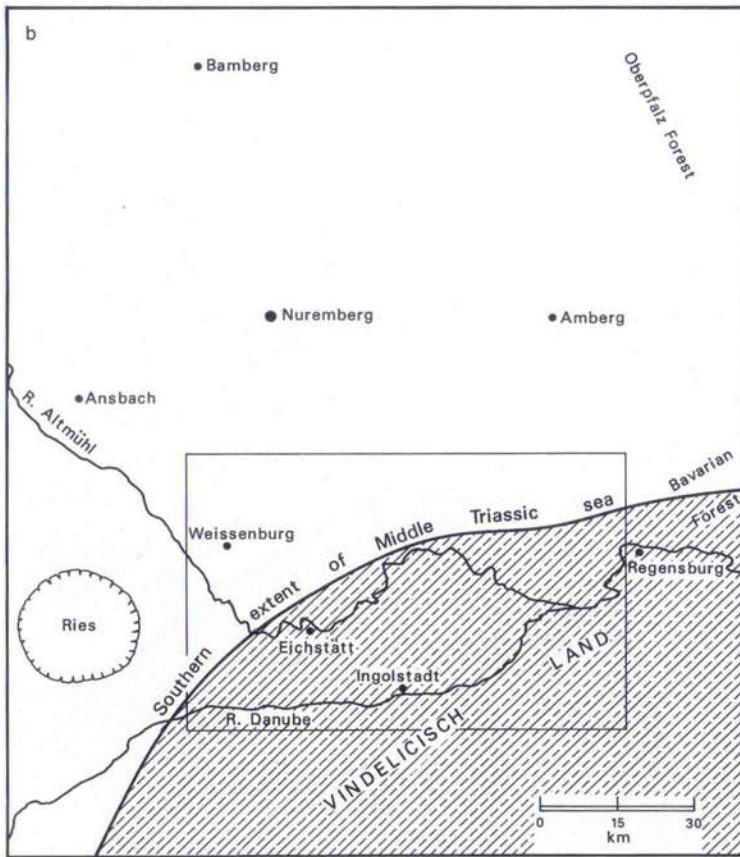
The debris which showered the surrounding country included material from uppermost Tortonian times back to the Triassic, as well as some Palaeozoic granite and gneiss. The crater and its recent sedimentary cover now delimits the outcrop area of the plattenkalk in the west.

From Upper Cretaceous times until the present day the Mesozoic sediments have been progressively eroded to form today's exposures. Several stages of limestone erosion or karstification can be recognized with caves at different underground levels in response to different levels of groundwater. The sediment which filled the caves, cracks and crevices is mostly reddish-brown clays, much of which is the local residue of dissolution of the impure limestones. Sometimes vertebrate fossils (bones and teeth) are preserved in the fissure fillings. For example, at Wintershof, near Eichstätt, there are numerous mammal remains in fissure fillings from the Burdigalian stage of the Miocene Period (25 Ma). With Tertiary uplift rivers cut down deep into the Jurassic
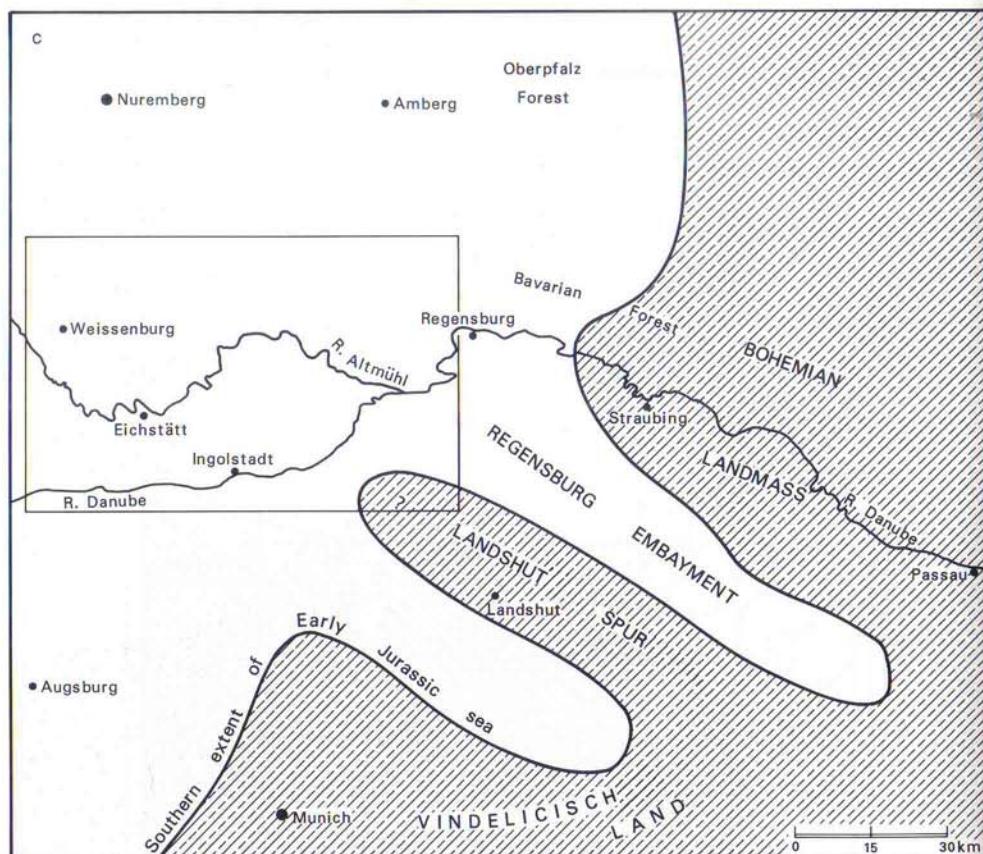
limestones. Deepest of all is the Altmühl valley which runs between Dollnstein and Kelheim. Although the present-day Altmühl river is too small to be responsible for such large-scale erosion, until the late Ice Age the valley used to guide the waters which now flow further south down the Danube valley. Throughout the Quaternary Period deep ground frosts further weathered the rock. At the end of the Ice Age men began to colonize the valley. The old caves in the valley sides provided protection and the Altmühl region is very well known for the many finds of prehistoric artifacts.

Palaeogeography and facies distribution in Late Jurassic times

Late in the Jurassic Period the Southern Franconian Alb was covered by a broad shelf sea which became progressively shallower and more isolated (see
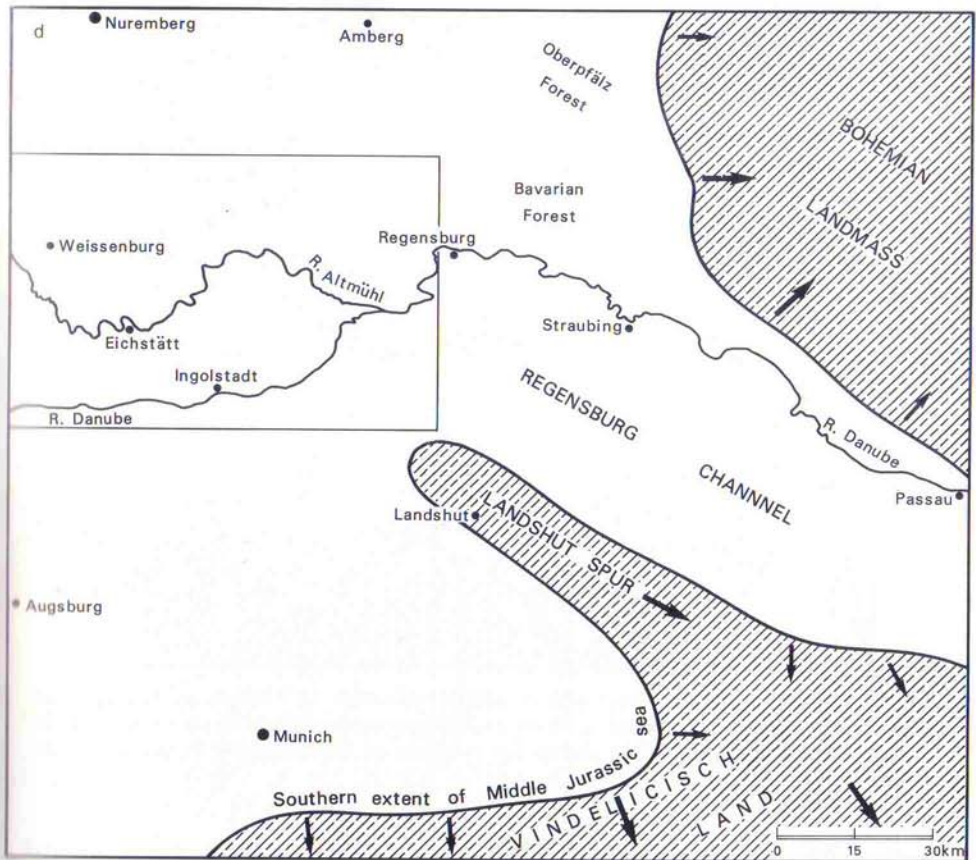
fig. 2.7, regional palaeogeography for Late Jurassic times). To the northeast lay the Bohemian Massif, to the north and northwest the emergent 'Mitteldeutsche Schwelle', and to the south a shallow-water platform, representing the submerged remnants of the Vindelicisch Land, which limited exchange of water with the Tethys Ocean. Channels connected the waters of the Tethys Ocean with those of the Southern Franconian Alb and along these conduits came Tethyan-type marine sediments and animals. The positions of these passages are uncertain but they are generally placed to the west and thus obscured under recent cover in the Ries Meteorite Crater. The Solnhofen water mass must also have been connected to the northern Boreal Ocean, because there are also rare boreal representatives in the Solnhofen fauna (Zeiss 1964).

Events leading to the formation of the plattenkalk basins began in Oxfordian times (see fig. 2.9a). In the west the deposition of regularly bedded argillaceous limestones, similar to those of Middle Jurassic times continued, and was

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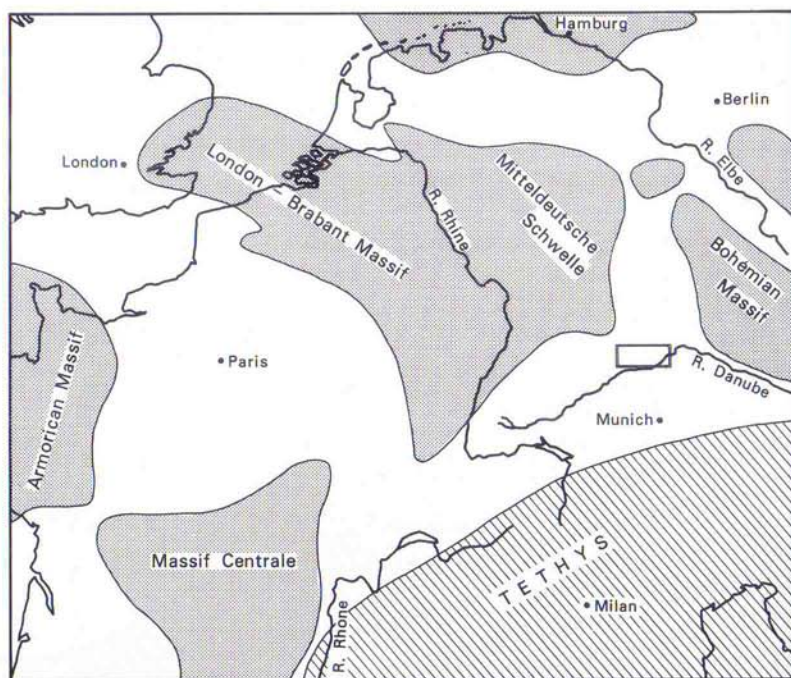
Fig. 2.7 General palaeogeography of northern Europe in Late Jurassic times. The shaded areas represent landmasses from a shallow continental sea on the margins of the Tethys Ocean. The small box shows the position of the Southern Franconian Alb. From Viohl (1985).

followed by purer limestones, whilst in the east a different facies was developed (a facies refers to an association of lithologies which are the deposits of a certain sedimentary environment). Slight submarine highs were colonized by an association of plate-like siliceous sponges and encrusted by cyanobacteria, between which were trapped peloids (amorphous lumps of calcium carbonate, some of which were perhaps originally faecal pellets), whilst at the same time lime mud (micrite) was deposited on adjacent areas of lower relief (fig. 2.8). On the highs, in the sponge–algal beds, not only was calcium carbonate produced at a faster rate, but this facies was cemented at an early stage making it resistant to compaction relative to the adjacent bedded micrites. A primary difference in relief between the sponge mound highs and intervening basins was thus accentuated. In most places the organically constructed mounds formed gently rolling submarine hills but where the mounds protruded more abruptly from the seafloor (as in the Kelheim area) chunks of debris occasionally fell from the edge of the reef mass into the surrounding bedded facies.

In the Kimmeridgian stage the sponges proliferated (figs. 2.9b, c & d and 2.10) and the barriers orientated along a NW–SE trend spread slowly north-
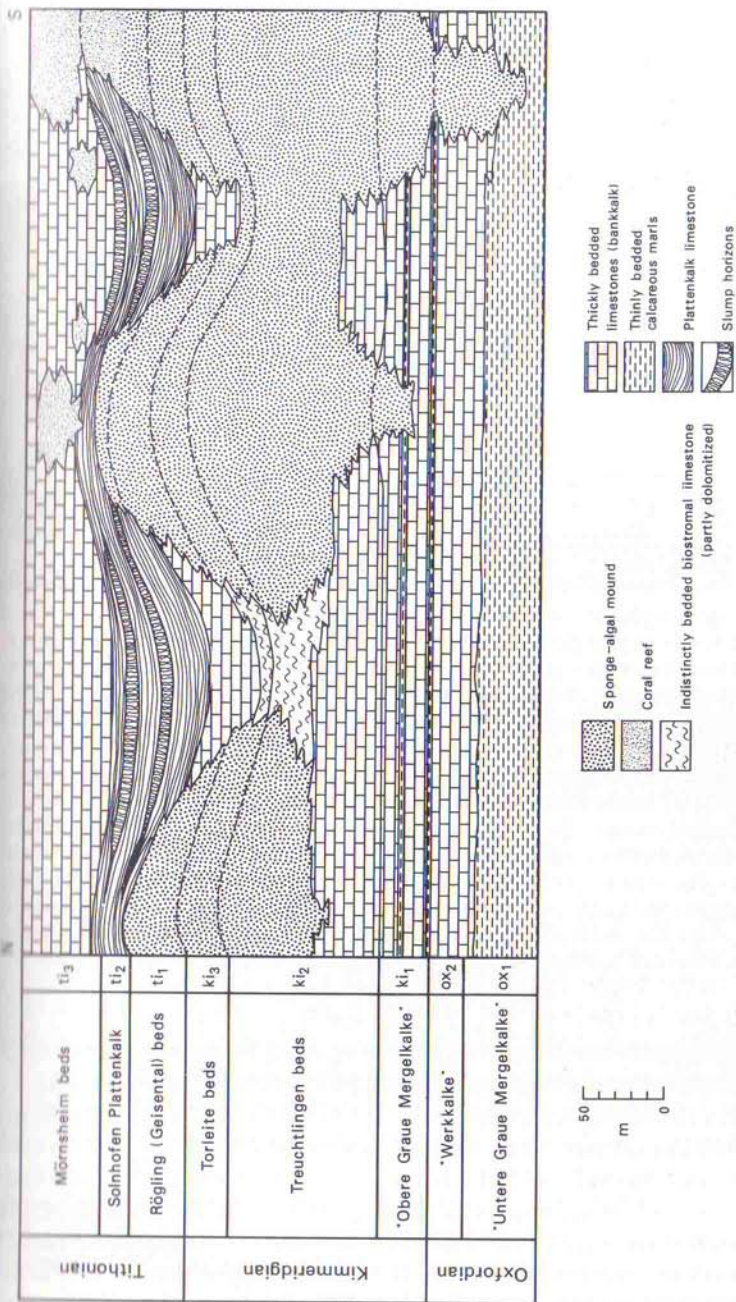
Fig. 2.8 Lithostratigraphy of the Southern Franconian Alb. Note how the growth of the sponge–algal mounds controlled deposition of the bedded facies. From Viohl (1985).

Tithonian	Mörnsheim beds	ti₃
	Solnhofen Plattenkalk	ti₂
	Rögling (Geisental) beds	ti₁
Kimmeridgian	Torleite beds	ki₃
	Treuchtlingen beds	ki₂
	'Obere Graue Mergelkalke'	ki₁
Oxfordian	'Werkkalke'	ox₂
	'Untere Graue Mergelkalke'	ox₁

Legend:
- Sponge–algal mound
- Coral reef
- Indistinctly bedded biostromal limestone (partly dolomitized)
- Thickly bedded limestones (bankkalk)
- Thinly bedded calcareous marls
- Plattenkalk limestone
- Slump horizons

Fig. 2.9 Palaeogeography of the Late Jurassic. The Southern Franconian Alb was a shelf area on the northern margin of the Tethys Ocean submerged under shallow water. During Late Jurassic times sponges colonized original highs in the underlying topography, building mounds which accentuated the relief of the seafloor. Protected basins were formed between the sponge–algal mounds and in these bedded areas limestones were deposited. (a) Oxfordian (ox_{1+2}) – start of sponge–algal mound growth in the east, probably as a result of shallowing. (b) Early Kimmeridgian (ki_1) – sponge–algal mounds spread westwards. (c) Middle Kimmeridgian (ki_2) – sponge growth reaches a climax and adjacent sponge–algal mounds fuse to leave intervening basins. (d) Late Kimmeridgian (ki_3) – water shallows further. Sponges spread to the bottom of the basins and appear in the bedded facies. Plattenkalk starts to be deposited in the east. (e) Early Tithonian (ti_2) – Plattenkalk is deposited over most of the Southern Franconian Alb. (f) Late Tithonian (ti_3) – sea starts to retreat and land emerges to the north. Plattenkalk is still deposited in the south. From Meyer & Schmidt-Kaler (1984) and from Meyer in Meyer & Schmidt-Kaler (1984).

wards. The chains fused into a network enclosing small basins which gradually shrank in size as they were overgrown by the rapidly accreting sponge mounds. The basins were first filled with bankkalk (*'Bankkalk'*), i.e. thick (dm to m) regularly bedded limestones, often rich in ammonites and with slightly undulose bedding planes. Bankkalk, like plattenkalk, has occasional thin intercalations of argillaceous limestones. The sponges spread to the bottom of the basins where they form a part of a bedded facies. One of the better kno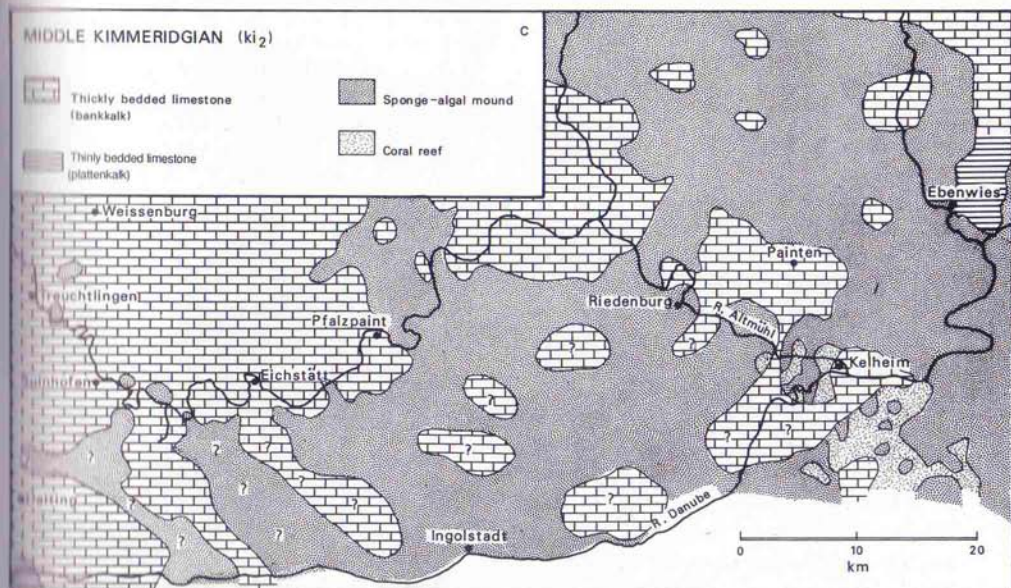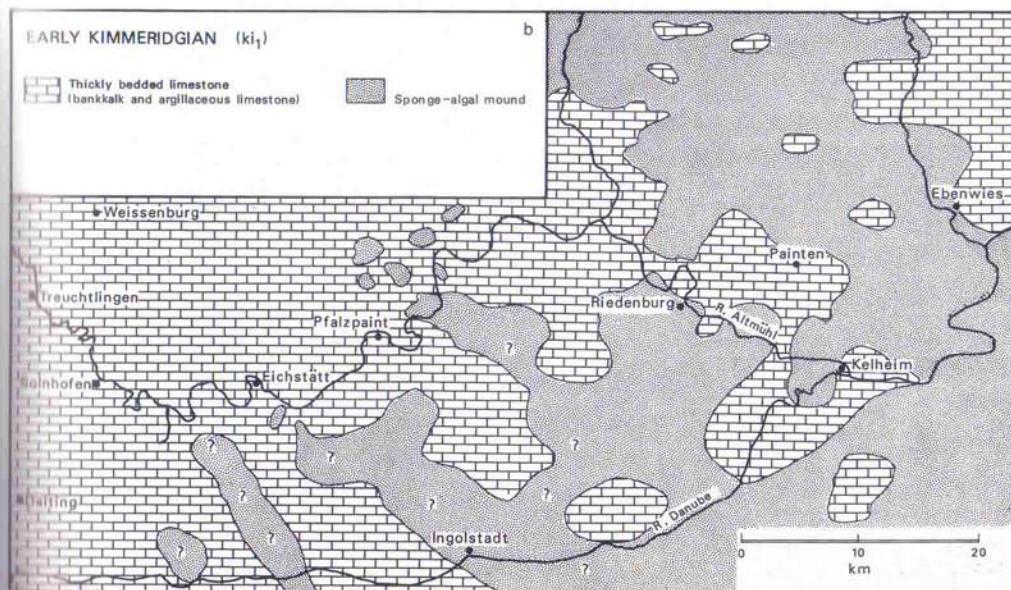wn of these deposits is the limestone known as the Treuchtlingen marble (*Treuchtlinger Marmor*), quarried around Eichstätt. Polished slabs display cauliflower-like structures where the siliceous sponges are covered by stromatolites (a sediment with characteristic wrinkly laminations on a millimetric scale,

(Fig. 2.9 parts d–f on pp. 30–31)

LATE KIMMERIDGIAN (ki₃)

Thinly bedded limestone (plattenkalk)

Thickly bedded limestone (bankkalk, argillaceous limestone, bedded sponge facies)

Sponge-algal mound

Coral reef

Weissenburg

Treuchtlingen

Pfalzpaint

Solnhofen

Eichstätt

Daiting

Ingolstadt

Painten

Riedenburg

R. Altmühl

Kelheim

Ebenwies

R. Danube

0   10   20
km

EARLY TITHONIAN (ti₂)

Thinly bedded limestone (plattenkalk and argillaceous plattenkalk)

Thickly bedded limestone (bankkalk, argillaceous limestone)

Sponge-algal mound

Coral reef

Weissenburg

Treuchtlingen

Pfalzpaint

Solnhofen

Eichstätt

Daiting

Ingolstadt

Painten

Riedenburg

R. Altmühl

Kelheim

Ebenwies

R. Danube

0   10   20
km

Fig. 2.10 Kimmeridgian sponge–algal mounds exposed along the banks of the Alt-mühl near Solnhofen. This facies weathers to form the cliffs and pillars. These are known locally as the '*Zwölf-Apostel-Felsen*'. From Meyer & Schmidt-Kaler (1984).

Fig. 2.11 Ammonite rollmarks from Painten; approximately half natural size; BSPHGM 1950 XXXV 15.

generally of cyanobacterial origin). There are also algal tubes, known as tubiphytes, ooids (smaller, rounded millimetric size calcareous grains which only form under conditions of fairly high energy), oncoids (spheroidal structures bounded by algae, generally requiring occasionally agitated water for formation), encrusting foraminifera (unicellular organisms building calcareous shells), as well as ammonites and much bioclastic debris. By Late Kimmeridgian (ki_3) times the water must have been quite shallow and wave motion fairly strong. Sedimentation was irregular, beds wedge out, and there are small unconformities where the processes of sedimentation were interrupted. In the reef facies horizons of oncoids, ooids and finely laminated (and wrinkled) stromatolites were formed. Another probable consequence of the shallowing was that the sponge mound facies began to be replaced by the bedded facies in the central part of the area, whilst in the east, near Kelheim, corals and hydrozoans colonized the tops of sponge mounds. The corals evidently built a stronger reefal framework than did the sponges and this gave

Fig. 2.12   Marks made by models of perisphinctid ammonites rolling over wet mud. Photograph by B. Kleeberg.

greater support to their accumulation. Thus the coral reefs grew steeply upwards, resulting in a narrow zone of growth mantled by a wider apron of debris.

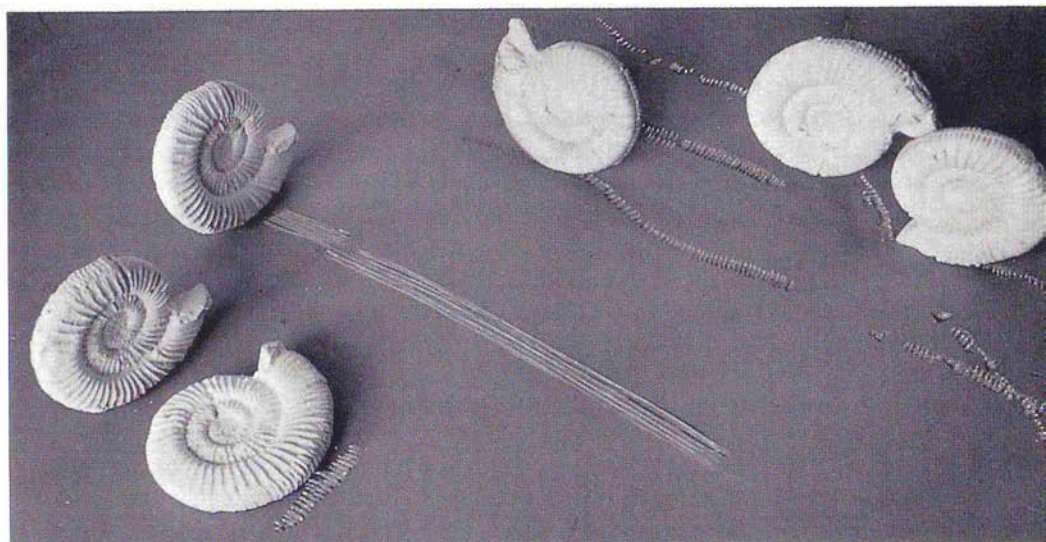With the shallowing of the water and an increasing importance of coral reefs as a barrier to the Tethys, the pattern of sedimentation began to change and the first plattenkalk was deposited in the eastern areas, a process which was to culminate in the deposition of plattenkalk at Solnhofen. Plattenkalk differs from bankkalk in the highly planar and much thinner (1–30 cm) nature of the bedding, although both plattenkalk and bankkalk may have thin intercalated beds of argillaceous limestone. The first major plattenkalk development occurred in Middle Kimmeridgian times (ki_2), far to the east at Ebenwies. The facies then migrated westwards as a response to the regional shallowing. By Late Kimmeridgian (ki_3) times plattenkalk was being deposited at Painten and Kelheim. Although superficially similar and with some beds containing exceptionally well-preserved fossils, overall this plattenkalk shows major differences to that of Solnhofen. There is a high concentration of preserved organic matter, which is often concentrated in layers of chert ('*Hornstein*'). The chert was probably derived from sponge spicules or planktonic radiolarians (unicellular microorganisms which secrete a skeleton of silica). This, together with the concentration of organic matter, indicates a high marine productivity (and as the Solnhofen area was not adjacent to any substantial land area the organic matter can not be terrestrial in origin (see palaeoecology, p. 73). The limestone fabric also contains numerous coccoliths (the calcareous plates of a unicellular alga, see fig. 3.7, pp. 44–5).

These earlier plattenkalks (of ki_2, ki_3 and ti_1, laid down before the main phase of plattenkalk development in ti_2) were probably deposited in an environment less isolated from the sea and more biologically productive than that of the Solnhofen Plattenkalk. The proximity of the coral reefs has also influenced the facies, most obviously as a source of detrital sediment which is interbedded with plattenkalk. In particular, as the reefs were flanked by steep slopes, sediment-laden currents could roll downwards depositing turbidite beds in the basin (Schairer 1968). The turbidite beds are graded and may show erosional structures at the base. These include scratches, gouges and impact marks excavated on the already consolidated seafloor by larger particles entrained in the flow. The underlying sediment was also scoured by local eddies forming hollows infilled by the turbidite sediment and now preserved in positive relief on the overlying infill as flute casts. Disc-shaped ammonites were bowled along in the strong currents (figs. 2.11 & 2.12). When the flow finally came to rest the larger particles, including the fossils and other fragments, were dumped first and covered by successively finer sediment producing the graded bedding diagnostic of such deposits.

Plattenkalk became more widespread as a facies from the beginning of the Tithonian stage. By this time the sea was sufficiently shallow and water exchange with the Tethys so restricted that conditions were no longer favourable for sponge growth. Corals had recolonized the tops of sponge mounds, forming a thick barrier in the east and isolated patch reefs to the south. As the sponge colonies died, leaving only the narrowest areas of sponge growth, the bedded facies encroached on the mounds. A map of the Southern Franconian Alb in Early Tithonian (ti_2) times (fig. 2.9e) shows a shelf covered by the sponge mound mass and peppered with small basins.

That these Early Tithonian facies were deposited in an environment which became increasingly restricted as time progressed is demonstrated by Keupp's (1978) studies of the microfacies. The rocks deposited in the early Early Tithonian (ti_1) begin with a red marl layer, the so-called '*Rote Mergel Lage*', a distinct marker horizon throughout the western area. It contains an abundance of recognizable plankton, mainly coccoliths and radiolarians, the latter contributing towards the chert horizons that pervade the limestone beds. The coccoliths are fairly well preserved and most probably originally lived in the overlying waters. The coccolith asemblages of the Red Marl Layer show that certain laminae are dominated by one species, *Cyclagelosphaera margereli*. At these times the environment must have been too hostile for other species, leaving only those which were the most tolerant to the extremes of salinity and temperature to inhabit the increasingly isolated 'lagoonal' waters. Moreover, because the coccolith assemblages are distinct from one thin lamina to another, this indicates an absence of bioturbation and macrobenthos from the stagnant bottom waters. A relatively high productivity of organic matter (in comparison with the Solnhofen Plattenkalk) led to anoxic, sulphidic conditions in the
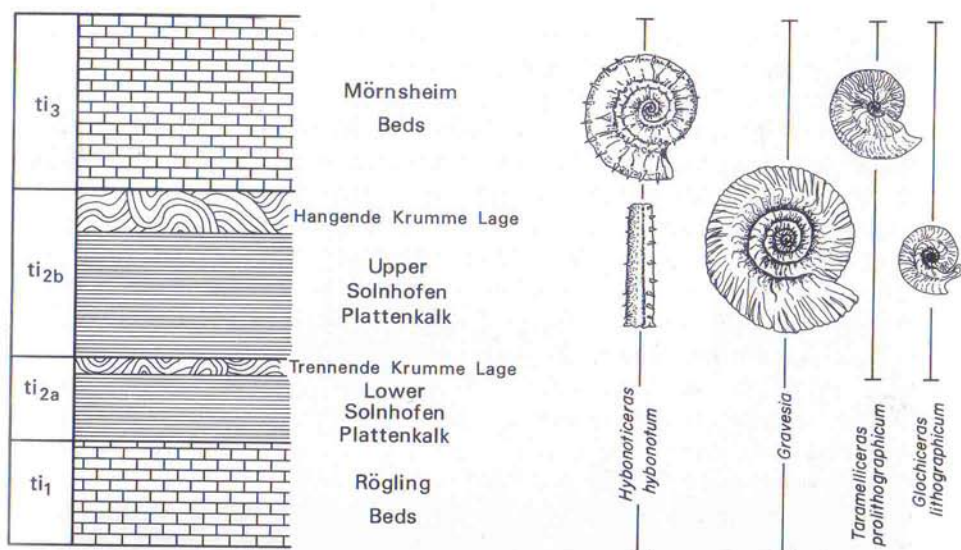
Fig. 2.13 Lithostratigraphic and biostratigraphic subdivision of the Tithonian beds in the Solnhofen–Eichstätt area.

stagnant bottom waters with the production of pyrite. It is the oxidation of this pyrite which has produced the red colour of the bed.

Somewhat surprisingly the environment seems to have been less hostile when the first plattenkalk was deposited in the Solnhofen–Eichstätt area (see fig. 2.13 for the stratigraphy of the Tithonian beds in this area). Thus the ti_2 stage sees the development in the Lower Solnhofen Plattenkalk (ti_{2a}) of a unit known locally as the '*Spurenschiefer*' (literally trace fossil shale, although it is in effect a thinly bedded limestone). This unit is more thinly and less regularly bedded than the Upper Solnhofen Plattenkalk, contains chert horizons and is filled with mottled, transecting marks thought to be trace fossils. These traces, combined with an irregularity in bedding and an absence of fine lamination, suggest that occasionally macrobenthos lived in the sediments of the basins. However, actual body fossils are rarely found.

In the later part of the Early Tithonian state (ti_{2b}) the plattenkalk reached the height of its development in the Solnhofen–Eichstätt area when the famous Upper Solnhofen Plattenkalk was laid down. The limestone is renowned for its planar, regular bedding and its pure carbonate composition as well as for the exceptional preservation of its fossils. In contrast to both the overlying (Mörnsheim beds) and underlying (Lower Solnhofen Plattenkalk) facies there is almost a complete absence of sponges and radiolaria so there are no chert horizons. Few microfossils are recognizable inside the limestone beds, whereas in the more clay-rich intercalations beautifully preserved coccoliths occur,
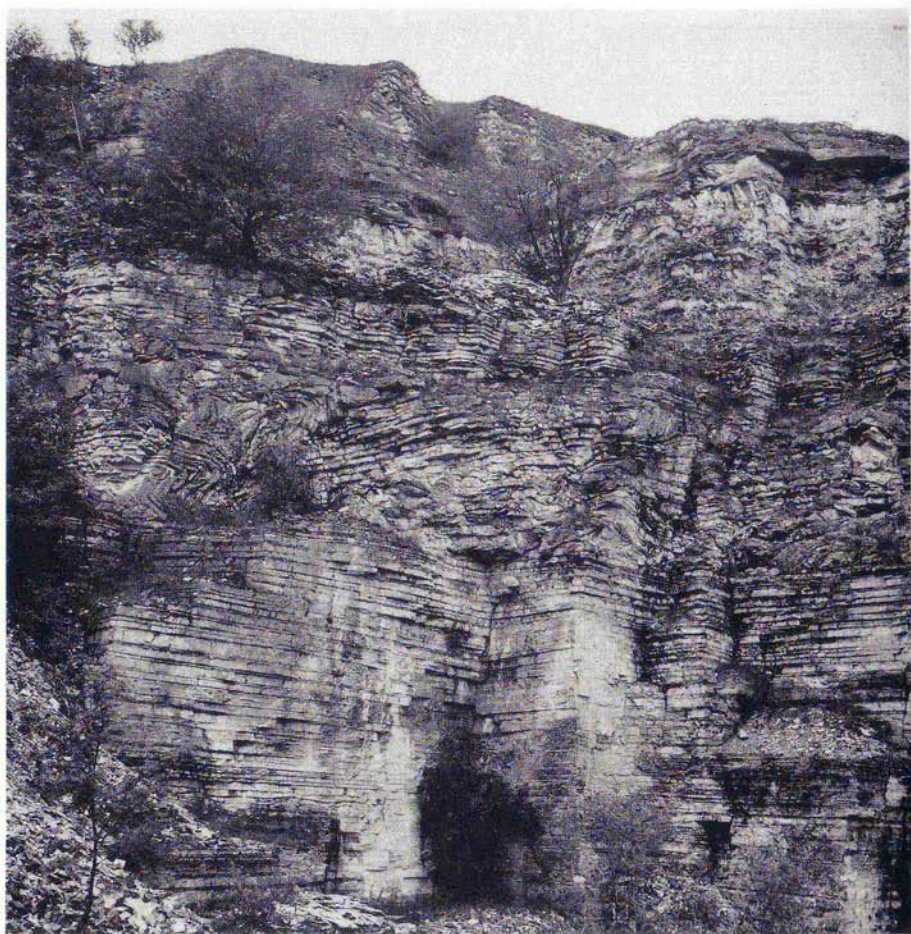
Fig. 2.14 Trennende Krumme Lage bed in the west wall of the Horstberg quarry, near Mörnsheim, south of Solnhofen. This slumped unit overlies the Lower Solnhofen Plattenkalk. (The Upper is thinly developed in this area.) At the top of this outcrop is bedded limestone of the Mörnsheim beds. From Meyer & Schmidt-Kaler (1984).

some of which are still articulated as coccospheres. These organisms probably grew in the lagoonal water, the hostile nature of which is demonstrated by the impoverished assemblages of coccoliths and foraminifera in terms of species and numbers.

As elaborated in chapter 4, most of the carbonate of the limestone beds was not formed in the essentially sterile lagoon but in the open sea by plankton and by the coral reefs. The marine carbonate ooze was resuspended by storms and transported over the reef with only the smallest particles being carried as far as Solnhofen. The fine sediment rained down onto an irregularly contoured basin

floor. In the Solnhofen–Eichstätt area, the gradient of this surface was not sufficient for the sediment to be destabilized by storms, and the plattenkalk beds are not thought to be redeposited by turbidity currents. (This had been advanced as a depositional mechanism and is discussed on p. 68.) It seemed to require a distinct shock to shift the semi-consolidated ooze and such events are recorded in the '*Krumme Lage*' beds, slump horizons which both underlie and overlie the Upper Solnhofen Plattenkalk (fig. 2.14). The Krumme Lage beds are composite, some 5–15 m thick and enclose a sequence of irregularly folded and sometimes broken units. The events which caused the sediment pile to collapse downslope were synchronous throughout a wide area and are best attributed to earthquakes. It was suggested by Keupp (1977b) that the occurrence of these slump horizons may be connected to movement along faults, which also affected water depth and isolation of the lagoonal waters.

Although the Upper Solnhofen Plattenkalk marks the top of the sequence at Solnhofen, in the Eischstätt area plattenkalk continued to be deposited until later in the Late Tithonian (ti_3) (fig. 2.9f), where it is included in the unit known as the Mörnsheim beds. In contrast to the Upper Solnhofen Plattenkalk, the Mörnsheim beds are rich in ammonites and bivalves, fragmented by wave action. Coccoliths are also common and some portions of the beds are siliceous because of the presence of radiolaria and sponge spicules. The sediments contain pyrite and the siphuncles of ammonites preserved in a black phosphatic material (so-called '*Sipho-Erhaltung*' which also occurs to a lesser extent in the Upper Solnhofen Plattenkalk) probably representing the build-up of anoxic conditions within the sediment due to a higher organic input. All this seems to indicate that connections with the Tethys Ocean had become re-established. Another plattenkalk from rocks of ti_3 age comes from Daiting, southwest of Solnhofen, and is well known for its well-preserved reptiles. In the southwest, between Monheim and Neuburg, plattenkalk was laid down at several intervals in the ages ti_{2-6}. East of the Solnhofen–Eichstätt area, in the Late Tithonian, there were accumulations of bankkalk, as well as deposits of argillaceous limestone and 'paper shale' ('*Papierschiefer*', or finely fissile argillaceous limestone). By the very end of the Tithonian (ti_6), marine deposition was evidently nearing an end and there is a clear coastal influence to the deposits as the sea retreated to the south.

3 Petrography of the Solnhofen Plattenkalk

Lithology in the Solnhofen–Eichstätt area

The most striking feature on entering one of the quarries in the Solnhofen Plattenkalk is the extraordinary regularity of the limestone. The beds are tabular and can be traced over several tens of metres with no change in their particular properties (colour, fracture, internal subdivisions and thickness), so much so that quarrymen can recognize individual beds and have even given them names (Edlinger 1964). On a scale of kilometres, between different quarries, the thickness of the beds varies. Where the plattenkalk is not thickly developed, such as at the edge of the shallow Eichstätt basin at Schernfeld, the beds occur in packets of thin sheets, each about 0.5–1.0 cm thick (fig. 3.1). In areas where the limestone accumulated to a greater thickness, as around Solnhofen itself, the limestone beds form units up to 30 cm thick (fig. 3.2). These slabs are quarried for use as lithographic printing stones on account of their thickness, purity and hardness.

The slabs of pure micritic limestone, given the name of *'Flinz'* by the quarrymen (plural *'Flinze'*, English adopted term, 'flinz'), may be interbedded by thinner (usually 1–3 cm thick) fissile, shaly layers, termed *'Fäule'* (plural *'Fäulen'*, English adopted term 'fäule'). Typical flinz beds are composed of a very pure calcium carbonate (95–98%), with only very minor proportions of clay (up to 3%) and quartz (up to 0.4%). In contrast, the typical fäule consists of 77–87% calcium carbonate, the rest being predominately clay (10–20%), with a small amount of quartz (around 3%). Lithologies intermediate in physical and chemical properties between fäule and flinz are also known, and given names such as *'Blätterflinz'* or *'zähe Fäule'*.

Stacks of flinz split into individual sheets along bedding planes, which are defined by surfaces where there is a concentration of clay minerals. Although flat, flinz slabs are not smooth, but slightly roughened, with the underside of the slab having smooth 'crenulations', whilst the topside has sharper ridges (fig. 3.3). These roughened textures may have formed during the de-watering of the sediment (Mayr 1967), or at a later stage in diagenesis. The difference in texture, which is most obvious in the purer and thicker beds, is useful because it gives an almost infallible criterion for the way-up of a slab. Weathered surfaces of flinz are a light yellow-white in colour and the beds break with a conchoidal

Fig. 3.1 Eichstätt plattenkalk facies at Neumayer quarry, 500 m NE of Schernfeld. The beds are typically 0.5–1.0 cm thick and separated from each other by clayey partings. From Meyer & Schmidt-Kaler (1984).

fracture to display a darker, beige-grey interior. Sometimes bedding planes may show other colours, such as concentric bands of yellow, brown or grey, or the beautiful fern-like markings called dendrites. Despite the plant-like appearance, these dendrites are inorganic features caused by a solution of the small amounts of iron or manganese from inside the beds and their reprecipitation as oxides along joint planes, cracks or around other discontinuities such as fossils (fig. 3.4). A fine lamination typifies the flinz from most localities in the Solnhofen–Eichstätt area. This appears either as a series of light and dark grey bands, on a scale of about 1 mm, or sometimes as more prominent but still diffuse white lines (fig. 3.10b) which probably reflect the effects of weak pressure solution. Where the white lines are continuous and well-defined, a flinz bed may split internally when hit hard with a hammer.

The sequence of flinz beds may be interrupted by the shaly intervals, usually around 1–2 cm thick, the so-called fäule (although the thin shaly laminae of only around 1 mm thickness which interrupt the stacks of flinz, may be included here). The colour is a yellow to medium brown, the exact tone depending on the clay content. The fäule splits like a shale into paper-thin
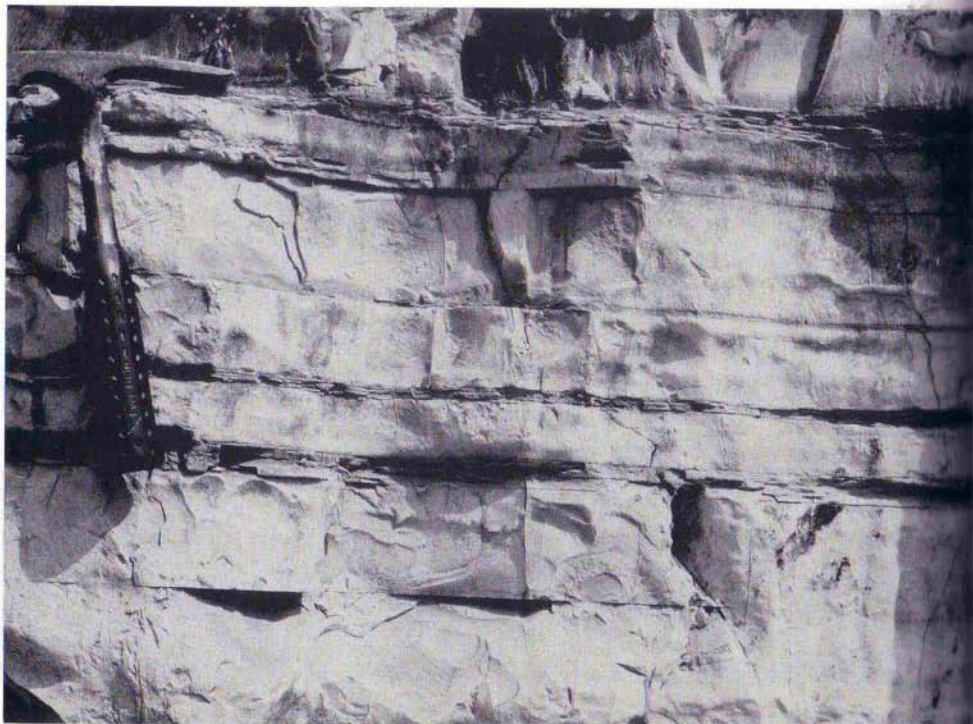
Fig. 3.2   Solnhofen plattenkalk facies at the Maxberg quarry, Solnhofen. The thick micritic limestone beds (flinz) may reach 30 cm thick and are intercalated with thinner beds of argillaceous, micritic limestone (faüle) 1–3 cm thick. From Meyer & Schmidt-Kaler (1984).

leaves which can be peeled apart. Beds of faüle weather recessively in the profile, so leaving the layers of flinz outstanding.

Occurrence of macrofossils

Flinz beds split apart along shaly partings and the fossils, when they are found, are almost always located on the underside of the slabs. The thin, microfossil-containing shaly lamina also sticks to the underside of the overlying slab. It might be suggested that the reason fossils are only found on bedding planes is that, even if they were present inside the beds, the well-indurated flinz slabs would not readily part to reveal them. However, certain peculiarities of fossil preservation counter this argument: fossils which show soft-part preservation are almost invariably accompanied by a depression in the bedding plane surfaces for several centimetres over the fossils. In the rare event of the fossils
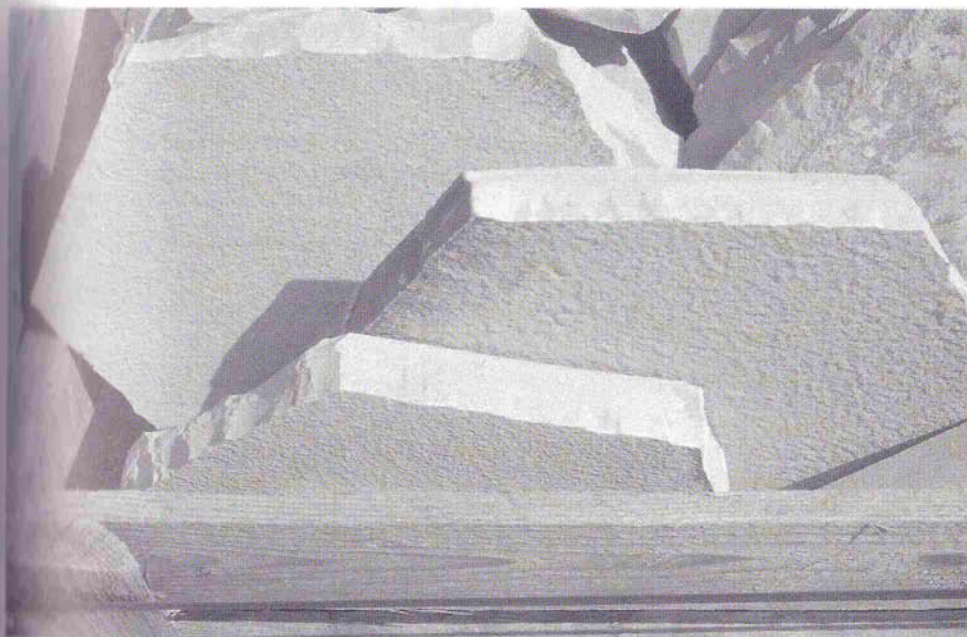
Fig. 3.3   Flinz slabs from Maxberg quarry, Solnhofen. The upper and lower slabs show the sharp ridges of the top surface of a bed whilst the middle one has the gentle undulations of a lower surface. Photo N. H. M. Swinburne. From Swinburne (1988), reproduced by kind permission of Elsevier Trends Journals.

causing an early concretion of the surrounding sediment, the opposite effect is produced, and a bulge occurs on the overlying bedding plane surface. These fossils would therefore certainly be visible if they were inside the slabs of flinz. Incidentally, the few fossils which have been found inside flinz beds can show a superbly detailed preservation.

Fäule fossils are also by no means uncommon but the higher the clay content of the limestone, the more the surface will peel away during surface exposure and destroy the fossil. The quality of fäule fossils is such that they are rarely kept in the public collections.

Grains and microfossils

Both flinz and fäule are so fine-grained that the electron microscope is needed to decipher the nature of the carbonate particles. Such observations show that grains in the flinz have to a large extent recrystallized, or are obscured by $CaCO_3$ overgrowths, with the cavities being filled with cement (although there is still a sufficient porosity (7–12%) to allow the stone to take up ink in lithography). A greater degree of success in the microscopic study of the

Fig. 3.4   Dendritic markings around a fish; *Gyrodus* sp., Eichstätt; maximum diameter 59 mm. IGPTUB, photo by B. Kleeberg.

sediment particles has been obtained from the beds of fäule and other shaly intervals, which are largely uncemented, and retain an original porosity of 14–26%. It has often been assumed that the carbonate in the flinz was originally the same as that in the fäule, but altered beyond recognition by diagenesis. This assumption is supported by investigations of the grain size of disaggregated flinz and fäule (Flügel & Franz 1967, Keupp 1977a) in that both flinz and fäule show the same major peak of 1–3 μm in the grain size distribution curve (fig. 3.5).

The first microfossils to be found in the fäule were foraminifera, discovered at the end of the last century. These benthic foraminifera (all with calcareous shells the size of fine sand, made by unicellular organisms which lived on the seafloor, see fig. 3.6) were described by Groiss in 1967 using light microscopy on samples of disaggregated fäule (see also comments on the nature of the assemblage, pp. 73–4). Assemblages of coccoliths (micrometre-sized calcareous plates which were originally the covering shields of a unicellular alga, called a coccolithophorid) were described by use of the electron microscope by Keupp (1977a) from the fäule and other shaly laminae (fig. 3.7). They occur
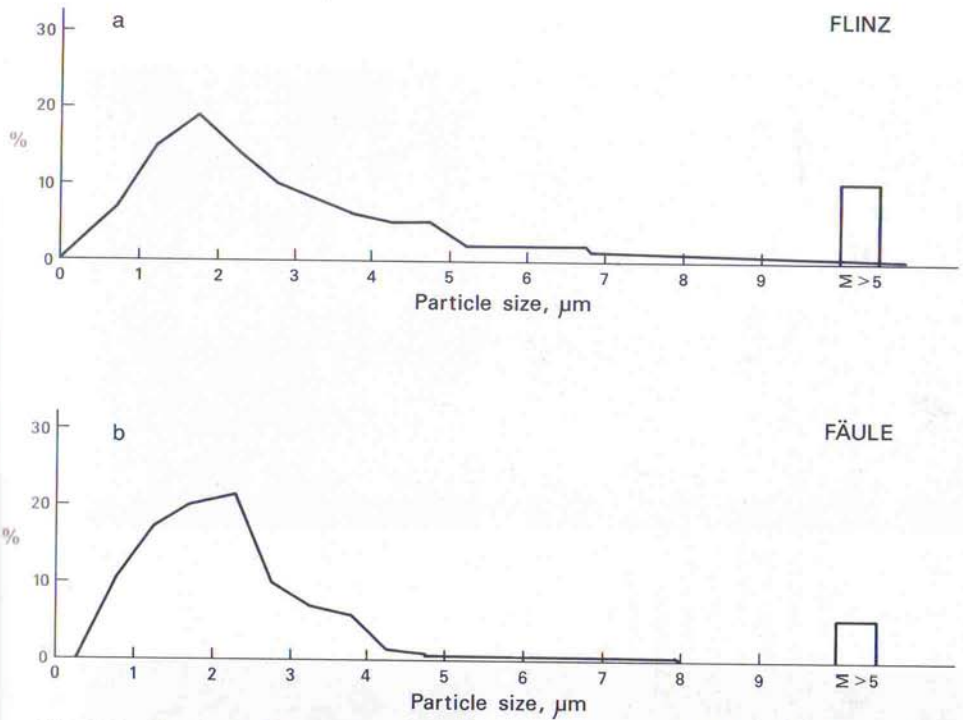
Fig. 3.5   Size frequency diagram of particle size of disaggregated plattenkalk. (a) Flinz from Maxberg quarry, Solnhofen; (b) fäule from Schernfeld. From Keupp (1977a).
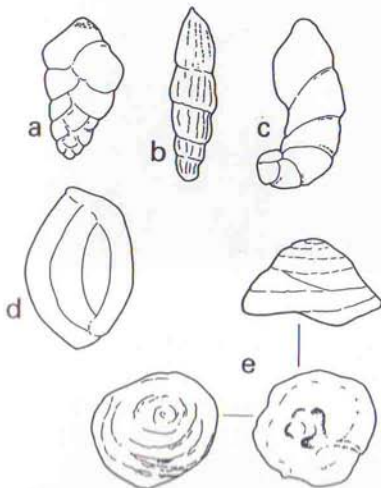
Fig. 3.6   Plattenkalk foraminifera. (a) *Gaudryina bukowiensis* Cushman & Glazewski (×42); (b) *Nodosaria eugly-pha* Schwager (×22); (c) *Marginulina distorta* Kusnetzowa (×40); (d) *Quin-queloculina egmontensis* Lloyd (×45); (e) *Patellina feifeli* (Paalzow) from above (left), from below (right) and from the side (above). From Groiss (1967).
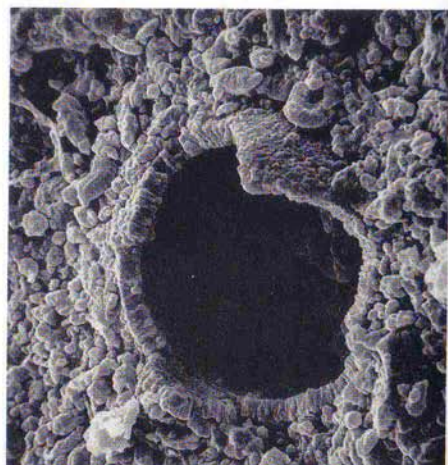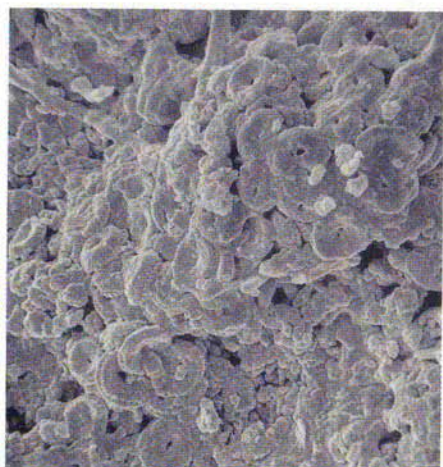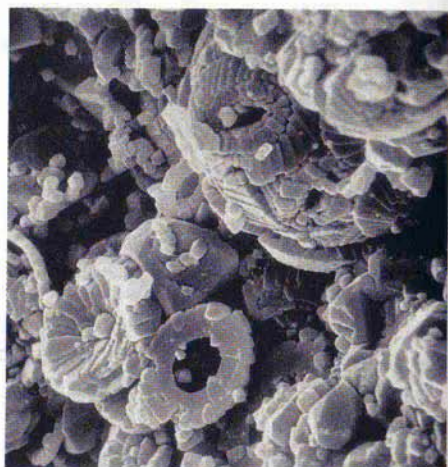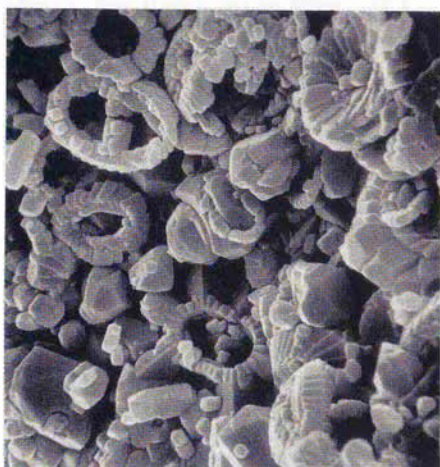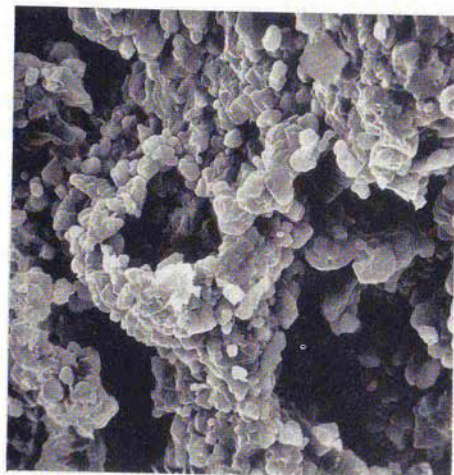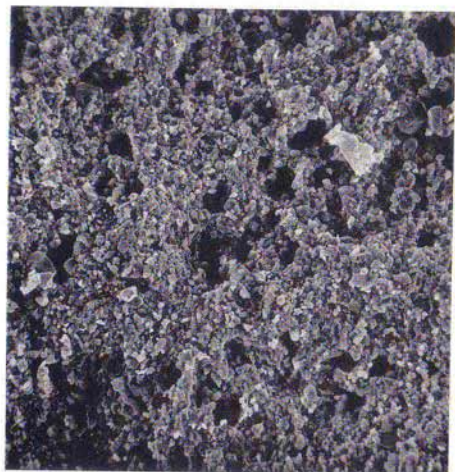
Fig. 3.7 Electron micrographs of the microfacies of the faüle (argillaceous limestone beds). (a) Isolated coccoliths; *Zeugrhabdotus, Stephanolithion, Ellipsagelosphaera* and *Cyclagelosphaera* from the Upper Kimmeridgian (ki₃) at Painten; field of view 14 μm. (b) Coccoliths in coprogenic aggregates; *Stephanolithion bigoti* Deflandre; field of view 31 μm. (c) Coccoliths in coccosphere; *Ellipsagelosphaera keftalrempti* Grün; field of view c. 13 μm. (d) Calcisphere; *Pithonella gustafsoni* Bolli from the surface of a faüle; field of view 28 μm. (e) Coccoid cyanobacterium; field of view 28 μm. (f) Rows of coccoid cyanobacteria concentrated along certain bedding planes. From Keupp (1977a).

predominantly in isolated aggregates some 50–100 μm in size (fig. 3.7b), suggesting perhaps that they are the remains of faecal pellets produced by animals such as crustaceans. Smaller accumulations of coccoliths, each having the same shape and so derived from a single species, may represent the *in situ* decay of a coccosphere (fig. 3.7c). Keupp also documents the occurrence of 'calcispheres' (fig. 3.7d), very regular spherical shells with a wall of radiating prisms (and quite distinct from the coccoid cyanobacteria, detailed below) which represent the cysts of calcareous dinoflagellates. (These are another group of protists named after the (unpreserved) pair of flagellae which they used for propulsion; the cysts are the resting stages of the life cycle.) The recrystallized remains of Radiolaria (protists with siliceous tests) are encountered only very rarely. Ostracods, submillimetric-size crustaceans, were described from the plattenkalk of the Langenaltheim area by Gocht (1973). The ostracods are preserved with both valves at right angles to the bedding (i.e. in life position), but are now crushed by the subsequent compaction of the sediment.

Keupp (1977a, b) has also described a suite of spherical cavities from the fäule which have an external diameter 8–20 μm, sometimes as much as 30 μm. According to Keupp, these cavities have a wall, typically 2–6 μm thick and built of rounded crystallites, each between 1 and 3 μm in diameter (figs. 3.7e, f). The internal diameter suggests it once enclosed a small cell and this cell probably secreted calcite rather than aragonite (there being no evidence of any widespread dissolution of unstable aragonite which would have infilled the cavities, nor of any relict aragonitic texture in the shell wall). These two lines of evidence suggested to Keupp that the spherical shells were secreted by the activities of coccoid cyanobacteria. Keupp considers that the cyanobacteria were the major contributors of the fäule carbonate because they are present in all fäule beds from the Solnhofen–Eichstätt area and even when the spheres themselves are not visible by use of the electron microscope the crystallites which make up the spheroid wall correspond closely in size to the measured grain size peak of 1–3 μm.

Others have pointed out that the walled cavities could be entire coccospheres (which would have a very similar diameter) with the individual coccolith plates too altered by recrystallization to be recognizable. In refutation of this suggestion Keupp (pers. comm. 1986) points out that rather than rounded crystallites which only touch at points, a system of interlocking plates should still be visible in the walls of broken spheres. Keupp (1977a) argues that although the micelles (the crystals which make up the coccoliths) are of the appropriate dimensions (1.5–3 μm), disaggregated coccoliths cannot be responsible for the grain size distribution for the following reasons. If the two coccoliths most common on the bedding planes of the Solnhofen Plattenkalk, *Ellipsagelosphaera* and *Cyclagelosphaera*, disaggregated they would produce micelles of two different sizes. Those derived from the inner whorl would be

equidimensional (less than 1 μm in size) and would dissolve under the weakest pressure solution. The resulting solution would reprecipitate directly onto the larger micelles which, although originally 1.5 × 3 μm, would grow in size as calcite precipitated in optical continuity, accumulating preferentially in the direction of the c-axis of the crystal so tending to elongate it. In this way the resulting rectangular grains would be long and thin, measuring about 6 × 1 μm. If, for some reason, the calcite which precipitated on the larger micelles precipitated on the sides of the grain tending to make it equidimensional, then the resultant particle would be too large (at 3–4 μm) to account for the observed grain size distribution. Finally, if in the unlikely event that the coccoliths, made of stable low-Mg calcite, suffered slight dissolution, so making them into rounded particles, then they would be too small in size.

Within the fäule, Keupp distinguishes carbonate laminae which contain these coccoid cyanobacterial cavities from the more shaly laminae which contain the diverse microfauna. Indeed, Keupp regards the fäule as a sequence of the shaly bedding plane laminae interbedded with thin carbonate laminae of the same composition as beds of true flinz (see Keupp's diagram of cyclicities, fig. 3.8). Others consider this alternation within the fäule as a secondary phenomenon due to diagenesis.

There is a divergence of opinion as to what constitutes the flinz (see plates of usual flinz appearance under the electron microscope, fig. 3.9). Many investigators have observed what they claim to be the remains of coccoliths, often disaggregated to single micelles, and showing to a varying extent diagenetic recrystallization and overgrowth. However, estimates of the proportion and distribution of these coccoliths varies greatly between different authors. For example, Flügel & Franz (1967) estimated there to be 500 000 coccoliths per mm^3. In contrast, according to Keupp (pers. comm. 1986), coccoliths make up a very minor fraction (some 1%) of flinz beds. Yet they attract attention because they are concentrated along certain laminae in the flinz which are minor planes of weakness. Keupp believes that, as with the fäule, the bulk of the flinz carbonate was precipitated *in situ* by microbial activity. In the flinz, unlike in the fäule, the moulds of cyanobacterial cells are not usually recognizable because the cavity of the cell has been infilled by cement. This blocky euhedral cement within the sphere breaks up on disaggregation to produce a tail on the flinz grain size graph of particles up to 15 μm diameter.

In addition to the presence of coccoliths, some larger particles have been observed in units of flinz (fig. 3.10a). Although still within the size range of micrite, this somewhat coarser fraction is termed 'reefal debris' by Hemleben (1977). He has observed fragments of foraminifera, bivalves, gastropods (with the brickwork-like texture of original aragonite remaining although now altered to calcite), ostracods, holothurian sclerites and other echinoderm remains. Under the light microscope the larger particles can be seen to be
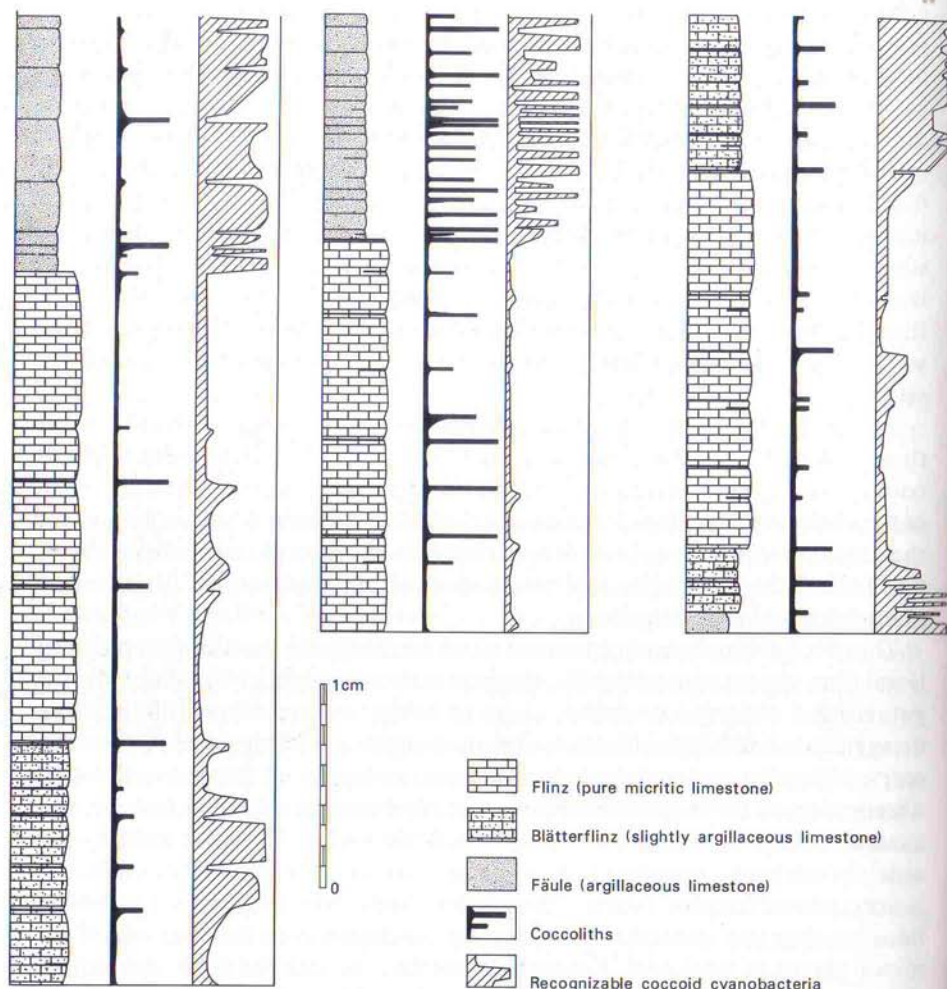
Fig. 3.8   Distribution of recognizable coccoliths and cyanobacteria in profiles from the plattenkalk at Schernfeld. From Keupp (1977a).

aligned in bands. Although usually planar, occasionally the lamination shows patches of small-scale cross-lamination (at least in some of the thick flinz of the Maxberg quarry, Solnhofen, fig. 3.10b) demonstrating the variation in energy conditions at the site of deposition. Hemleben also recorded a disruption of the lamination and the occurrence of dark blotches which probably represent small-scale bioturbation (fig. 3.10a). Some flinz units from the Solnhofen–Eichstätt area may show coarser particles at the bottom of a bed grading to finer particles, many of them coccoliths, at the top.
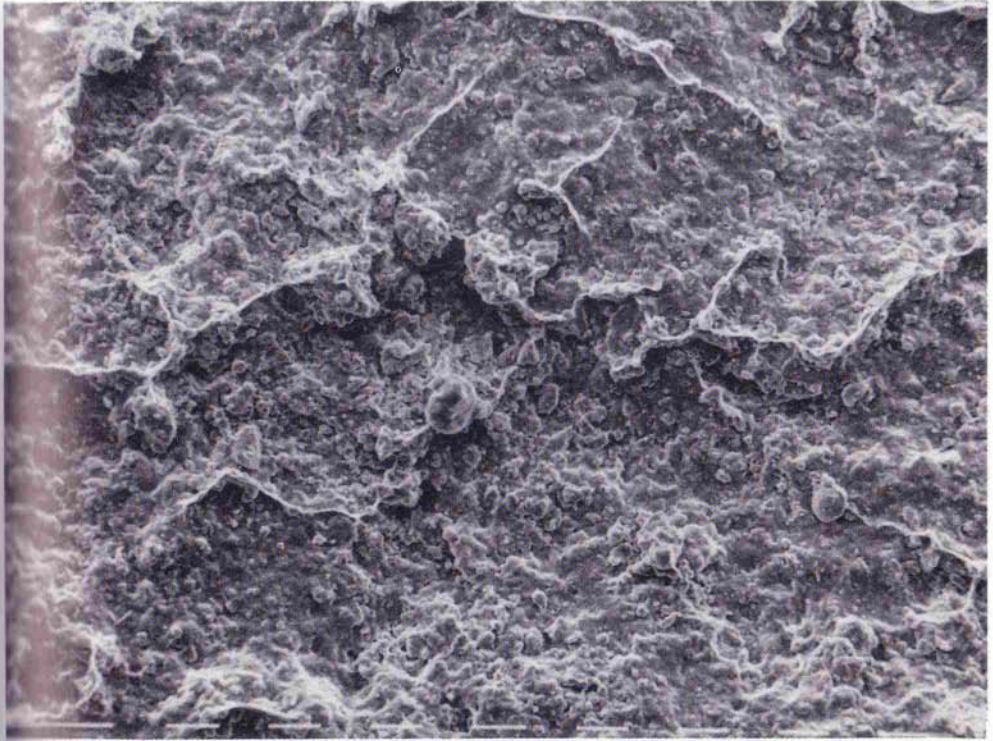
Fig. 3.9 Typical appearance of Solnhofen Plattenkalk under the electron microscope. Picture of the underside of a slab of flinz from Wintershof, Eichstätt. Note the reticulate pattern of ridges with a few scattered coccoliths. Scale bar 10 μm. Photo N. H. M. Swinburne.

Diagenetic alteration of the sediment

To recap the properties of the flinz: this effectively pure carbonate is extremely fine-grained and seems to have been severely altered during diagenesis. Even with the electron microscope, it is very difficult to see any shape or texture in the carbonate grains which would reveal their original form. Whilst most of the particles are probably the broken remains of coccoliths which had accumulated on the seafloor, others would have been the finest of the abrasion products derived from the reefs. The more clay-rich fäule may have had an additional source of carbonate, that produced *in situ* on the lagoon floor by cyanobacteria.

Indistinguishable to the eye, different grains of calcium carbonate may differ in mineralogy and chemistry. There exist two main varieties of calcium carbonate, calcite and aragonite, each with a different crystal structure. Both may form at the earth's surface, but aragonite is metastable and in the
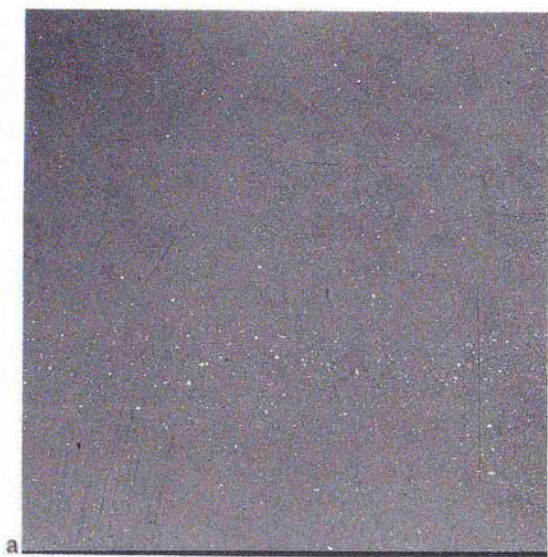
particular physical and chemical conditions encountered during burial, aragonite is transformed to the more stable form, calcite. Both minerals are slightly impure calcium carbonates which incorporate other similarly sized and charged ions into their crystal structure in the place of the Ca^{2+}, most especially Mg^{2+}. Measurement of the magnesium content of biologically as well as inorganically produced calcite defines two groups of calcite, a low-magnesium (Mg <3%) and a high-magnesium (Mg >3%, sometimes as much as 25%) variety. Diagenesis is driven by the relative chemical instability of high-Mg calcite and aragonite with respect to low-Mg calcite and it produces physical changes in the sediment fabric.

As the mud ooze of the plattenkalk was compressed, the carbonate grains came into contact and ultimately, under sustained pressure, they dissolved at the contacts by the process of pressure solution. The particles became welded into a sturdy, supporting framework. Pointed and protruding corners were especially prone to dissolution, and originally angular particles (such as the rectangular crystals of coccoliths) became rounded. Small low-Mg calcite fragments, together with any aragonite and high-Mg calcite, which were also relatively unstable, either recrystallized or dissolved. This provided a $CaCO_3$-rich fluid which could precipitate as overgrowths (usually in continuity with the existing crystal structure) or migrated through the $CaCO_3$ framework, and infilled the cavities with a blocky cement. Later, some rhombs of dolomite ($CaCO_3.MgCO_3$) grew within the sediment. The rhombohedral cavities in some flinz beds are clearly holes where dolomite crystals have been dissolved away (e.g. Keupp (1977a), p. 70, pl. 24, figs. 1–3 and Mäuser (1988)). The net result of these diagenetic processes was to convert a once soft sediment into a compact and tough rock.

Whilst the flinz carbonate remains something of an enigma, in the fäule well-preserved carbonate microfossils can be clearly seen. The difference in preservation between those coccoliths found in the flinz and those in the fäule can mainly be attributed to the higher clay content of the fäule (but there may be other sedimentary differences). This prevented the calcareous particles from pressing against each other and the clay also reduced the permeability of the bed. Pore fluids could not penetrate unfilled voids between the microfossils and precipitate overgrowths of $CaCO_3$. Consequently the fäule now has a higher porosity than does the flinz.

The laminations in the fäule and to a lesser extent in the flinz have been enhanced by the effects of pressure solution (see fig. 3.10b). Flinz/fäule boundaries and the surface of the fossils have also been affected. Pressure

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Fig. 3.10   Optical micrographs of Solnhofen flinz. (a) Dark blotches represent bioturbation by *Chondrites*; the light-coloured particles are larger particles of reefal debris (×10). (b) Lamination, planar to flaser, enhanced by pressure solution (×2). From Hemleben (1977).

solution of the carbonate was concentrated along a bedding or a lamination surface across which there was a change in solubility of material, perhaps due to differences in particle size or mineralogy. Any insoluble residue, such as the clay, remaining after dissolution of the carbonate compacted together to form an irregular surface. In section this is seen as a thin jagged line, known as a stylolite. The greater the number of solution surfaces, the more carbonate has been removed, so increasing the percentage of clay still further. The contrast between almost pure micritic flinz and marly fäule must have been heightened by such diagenetic effects, but the extent of this process remains uncertain. While Keupp claims the effect to be minimal, Hemleben (pers. comm. 1986) suggests that migration of carbonate out of fäule into the flinz beds could have led to substantial increase of flinz thickness. Other smaller-scale cyclicities may also be diagenetic in origin. In particular the rhythmic alternation of clayey and carbonate laminae within the fäule, commented upon by Keupp, may be the result of a secondary separation of the components. Similarly Keupp's observation of a restriction of coccoliths to distinct bands in the flinz is, in Hemleben's opinion, merely a consequence of coccoliths being obscured by diagenesis elsewhere in the flinz.

Redistribution of elements

The now lithified limestone consists almost entirely of low-Mg calcite, but there are still indirect methods to establish the original types and origins of the calcium carbonate particles. The geochemical arguments used by Veizer (1977) to estimate the original constitution of the sediment were based on the distribution of the element strontium which, like magnesium, is a minor impurity in the calcium carbonate lattice. In the crystal structure of aragonite more strontium is permitted in place of calcium than can be held by either high-Mg or low-Mg calcite. Consequently, when this aragonite is dissolved during diagenesis it will enrich the pore-waters in strontium. If the fluid reprecipitates as a pore-filling cement it will have a high-Sr composition. So a sediment that originally contained some aragonite, but has now been completely altered to calcite, would be expected to contain a higher concentration of strontium than would a sediment derived from a high-Mg calcite alone, if that sediment merely redistributed the elements internally.

However, in reality the sediment and pore fluids do not form a self-contained chemical system. During diagenesis there is some chemical exchange of pore waters with other reservoirs. These reservoirs include the overlying seawater and marine or fresh (meteoric) water trapped in the pores in the overlying rock formations. During such exchange, much of the strontium (as well as magnesium) in the pore waters can be lost to the system. To assess the possible extent of contamination of the system by meteoric water, a method exists that

depends on the measurement of stable isotopes of oxygen, ^{18}O and ^{16}O. The ratio of these isotopes in meteoric water is lower than it is in marine water (how much lower is mainly dependent on the latitude of the site of deposition). The measured values of oxygen isotopes are generally expressed by the delta notation whereby the ratio is expressed relative to an agreed standard (a belemnite from the Pee Dee Formation in South Carolina, USA).

$$\delta^{18}O = \frac{(^{18/16}O_{sample} - {}^{18/16}O_{standard})}{^{18/16}O_{standard}} \times 1000$$

By comparison to today's rainfall belts, the Solnhofen meteoric water of Jurassic times most probably had an isotopic value of between −2 and −5 ppt, whilst the original calcium carbonate which formed in marine waters would have had values which were around zero. The graph in fig. 3.11 shows the change in $\delta^{18}O$ of the carbonate versus strontium content for three original types of sediment: a low-Mg calcite, which is relatively stable, and the unstable high-Mg calcite and aragonite. As explained above, these unstable components are liable to dissolve and recrystallize during diagenesis producing carbonate pore fluids that are relatively rich in strontium. These pore fluids then migrate out of the rock usually to be replaced by meteoric water with little Sr and negative $\delta^{18}O$. Thus, as exchange proceeds, strontium is removed from the rocks and the extent of the process is also recorded by an increasingly negative oxygen isotope signature. The strontium content of the flinz carbonate was measured by Veizer (1977) at about 150 ppm, and an average value of $\delta^{18}O$ as −3.5. He explained this by the diagenesis of a sediment containing
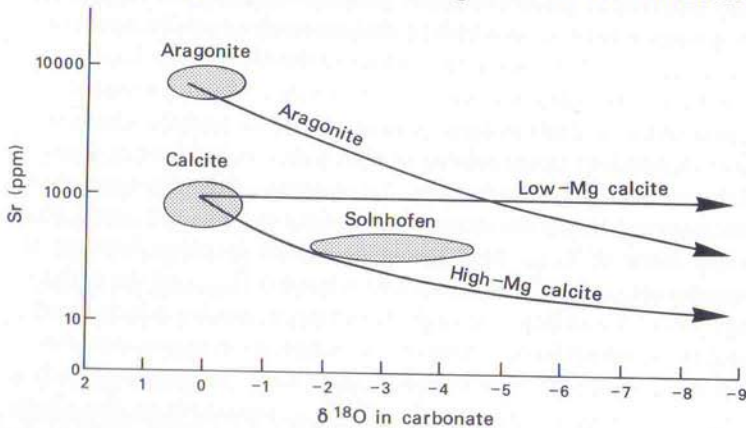
Fig. 3.11 Path of diagenesis for aragonitic and calcitic sediments in contact with meteoric water. As aragonite and high-Mg calcite recrystallize to low-Mg calcite under the influence of meteoric water, strontium (Sr) is expelled from the calcium carbonate lattices. The extent of recrystallization can be determined from the changing oxygen isotope values which become progressively more negative (enriched in ^{16}O) as diagenesis proceeds. Adapted from Veizer (1977).

about a third low-Mg calcite, which was mainly coccolith pieces. The other two-thirds could be either aragonite or high-Mg calcite (or a mixture of both), and probably represents the 'reefal detritus'. In fairness, it should be added that since this work much more has been learned about the partitioning of the element strontium in carbonates and many researchers consider diagenetic effects to swamp original differences.

Another element besides oxygen with isotopes which behave differently during geological and biological cycling is carbon. Carbon is represented by ^{12}C, the most abundant isotope, ^{13}C, a rather stable isotope, and ^{14}C, a short-lived radioactive isotope (with which we are not concerned in rocks of this age). It is the ratio of $^{12/13}C$ in a carbonate which can give crucial information about its origin.

As with oxygen, values of carbon isotopes are expressed by a delta notation where they are referred to a standard, usually that same Cretaceous belemnite.

$$\delta^{13}C = \frac{(^{13/12}C_{sample} - {}^{13/12}C_{standard})}{{}^{13/12}C_{standard}} \times 1000$$

In the sea, carbon, in the form of carbon dioxide dissolved in the surface waters, is taken up by green plants during photosynthesis, and incorporated into carbohydrates. The organic matter is eventually broken down, either in the water column, or in the sediment, to form carbon dioxide again. During each of these stages in the carbon cycle, the ^{12}C and ^{13}C become fractionated; in photosynthesis plants preferentially incorporate the lighter ^{12}C into organic matter ($\delta^{13}C_{org} \simeq -27$) and the carbon dioxide remaining in seawater grows isotopically heavier as photosynthesis proceeds. When the organic carbon is broken down again (a process which in shallow-water environments takes place mainly on the sediment surface), the lighter carbon is returned to the system, so diluting the heavy inorganic carbon in the seawater. Marine invertebrates build shells by precipitating carbon dioxide into carbonate and the shells will have a $^{12/13}C$ ratio dependent upon where in the water column they grew and the extent of the carbon cycling processes. An example of the application of carbon isotope measurements comes from foraminifera in deep-sea cores. Planktonic foraminifera have $\delta^{13}C_{carb}$ around +0.5, which is often heavier than the benthic species whose calcareous skeletons have $\delta^{13}C_{carb}$ of the order of -0.5. There may also be a difference in $\delta^{13}C$ between species which lived in open marine and those which lived in poorly oxygenated environments. An accumulation of degrading organic matter will tend to make the inorganic carbon in the bottom water, and consequently the $\delta^{13}C_{carb}$ signature in the shells more negative. Yet, as with all isotope and trace element studies, diagenesis is a complicating, and some would say overwhelming, factor. The carbonate recrystallizes and its original $\delta^{13}C$ is changed, or else cements with different $\delta^{13}C$ values are added to a rock making the 'whole rock' $\delta^{13}C$ value of debatable significance. However, carbonates with very negative signatures are

often those which were buried in an organic-rich sediment. (For a fuller discussion of carbon isotopes, the reader is referred to the SEPM short course booklet, edited by Arthur *et al.* 1983.)

Carbon isotope values for the carbonate of the flinz beds of the Solnhofen Plattenkalk are in the range −1 to +2. Indeed, a block of Solnhofen Plattenkalk was used as a standard for calibration of mass spectrometers for carbon isotopes on account of its pure $CaCO_3$ content (see Craig 1957). We have obtained some measurements on flinz and fäule from the Maxberg quarry, Solnhofen (N. J. Shackleton, pers. comm. 1986). The flinz gave values of $\delta^{13}C = +2$ ($\delta^{18}O = -3.8$) and the adjacent fäule was slightly heavier at $\delta^{13}C = +2.5$ ($\delta^{18}O = -4.2$). (This cannot be purely a diagenetic effect, or the flinz would be expected to have a more negative oxygen isotope signature than the fäule. However, the detailed geochemistry of this effect would take us beyond the scope of this book.) These results are exactly what would be expected from a carbonate made of coccolith pieces, mollusc debris, foraminifera, etc. laid down in an oxic milieu. They are not commensurate with an accumulation of dead coccolithophorids at the bottom of an anoxic water column (as de Buisonjé suggested, see pp. 63–4) because the large amount of organic matter in the sediment would yield much more negative results for the bulk carbonate. Whether or not these values could be obtained from a carbonate which was precipitated by the activities of benthic cyanobacteria under a hypersaline water column is still an open question. The only relevant data apparently available for comparison come from recent algal mats of Solar Lake, Sinai. Values of $\delta^{13}C = +3.5$ have been measured in the carbonate which has been precipitated around cyanobacterial cells (Schidlowski & Matzigkeit 1984). Here the cyanobacterial spheres are only forming under the surface of the mat, in the zone of decay (Krumbein *et al.* 1977), but, because the carbonate has a positive rather than a negative signature, it cannot be derived directly from the carbon of the cyanobacterial organic matter. Instead, the carbonate is probably induced to precipitate because of the alkaline conditions produced during decay, the source of the carbon being that present in the seawater that had remained after photosynthetic depletion, i.e. relatively heavy carbon. Being highly hypersaline, the cycle of carbon isotopes in Solar Lake is very atypical of modern marine environments, the organic matter being very little fractionated from normal seawater, with values of −5.7 (rather than around −27) being recorded (the amount of dissolved carbon dioxide is very low and actually limits the rate of photosynthesis). Indeed, the final value of $\delta^{13}C$ depends greatly upon the salinity of the environment and the age of deposit (due to secular changes in the $\delta^{13}C$ of seawater) as well as the amount of organic matter finally preserved (W. E. Krumbein, pers. comm. 1987). All that we can conclude at present is that the carbon isotope values in the Solnhofen Plattenkalk do not exclude the role of cyanobacteria in forming some of the carbonate.

4 Palaeoenvironment and sedimentation

Palaeoenvironment

So regular, so tabular, were the sheets of lime mud that became the plattenkalk that it can only be concluded that they were laid down in very quiet and protected waters. This view has not always prevailed. Early depositional models envisaged the Southern Franconian Alb as a vast mudflat where sediment was brought onshore by storms to dry out and consolidate under the sun. With this picture in mind, early investigators misidentified the trace fossils as the tracks of walking birds or reptiles. Under such a model the process of special preservation was seen as a kind of 'mummification' with corpses lying on the shore drying out in the sun. Even if this could have been true for some of the land reptiles, it is not an adequate explanation (see under biostratinomy of the terrestrial biota, p. 93) and is anyway redundant in the case of the exceptional preservation of the marine fossils.

The plattenkalk sediment shows no features to support hypotheses of subaerial exposure. If deposition of the plattenkalk had taken place on some kind of mudflat that was periodically emergent, then the sedimentary sequence might be expected to contain diagnostic sedimentary structures. Features such as channels eroded by tidal currents, widespread deposition of cross-laminated sediment and other related sedimentary structures are noticeably absent. Moreover, in the intensely arid climate (see p. 93) the mudflat would surely have dried out, and there is no evidence for evaporites or any other features of a sabkha-type setting.

The restricted basin model

It is now generally agreed that the plattenkalk basins lay permanently submerged under a stable body of water. However, the basins cannot have been landlocked. There must have been some connection to the sea as most of the fossils are of the bodies of marine organisms, broadly similar to species living today in tropical reef environments. Part of a coral reef, of Late Jurassic age, is to be found south of the Solnhofen area, now exposed along the banks of the Danube. The Late Jurassic corals almost certainly lived, as do most modern

corals, in the well-illuminated surface waters of a shallow sea. That sea must also have been near to the land to receive the bodies of land reptiles and insects. The Solnhofen area may then be thought of, in a broad sense, as a lagoon bordered to the north by low-lying land and to the south by a chain of coral reefs which protected it from the turbulence of the Tethys Ocean (fig. 4.1). The base of the lagoon was covered by dome-shaped mounds, built by sponges and cyanobacteria (blue–green algae) in the Kimmeridgian stage of the Late Jurassic). The mounds shielded intervening hollows from the effects of currents and, in the quiet basinal waters, the plattenkalk sediment was deposited.

There are various ways to estimate the depth of water in the plattenkalk basins, all relying on different assumptions. Firstly, by assuming that the
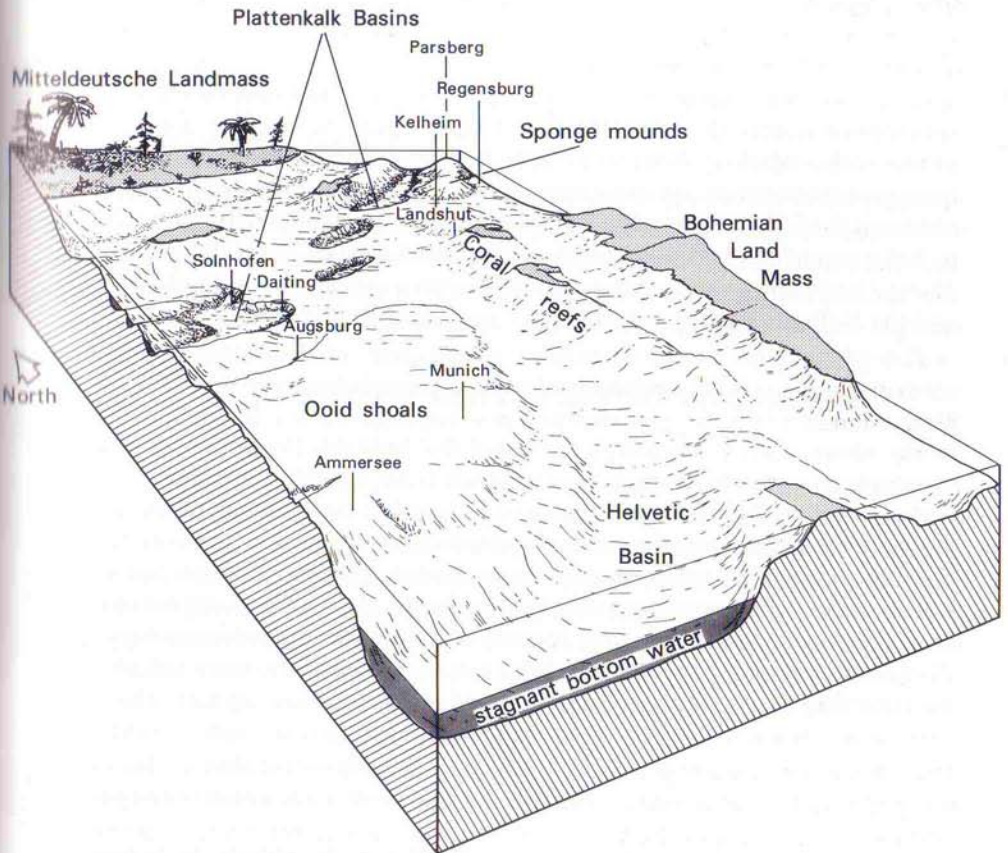

Fig. 4.1 Palaeogeography of the Solnhofen area in Tithonian times. The Solnhofen shelf with its sponge–algal mounds and intervening basins was bordered by land to the north and east and, across an ooid platform, by the deeper waters of the Tethys Ocean in the south. Redrawn from Meyer in Meyer & Schmidt-Kaler (1984).

Jurassic coral reefs grew in environments similar to today's coral reefs, the most active zone of reef growth would have been under about 10 m of water. It also seems plausible that the sponge–algal mounds were shallow-water features, possibly protruding above the surface of the lagoon as islands and separating deeper basins. The relative depth of the basin can then be calculated from stratigraphic sections, bearing in mind the relative amounts of compaction between sponge–algal mound and bedded limestone facies. Barthel arrived at values for the water depth of 30–60 m. Similarly, the water depth in the basin could be estimated roughly by knowing the depth of water in which the sponge–algal mounds grew.

Another constraint on water depth is provided by the cyanobacteria thought to have formed a mat over the sediment surface. Cyanobacteria reflect the blue–green wavelengths of light (hence their alternative name of blue–green algae) whilst using the red for photosynthesis. As the red is the long-wave end of the visible light spectrum this colour is first to be absorbed when passing through the water column. Accordingly, it is estimated that in these clear, subtropical waters the intensity of red light would be too low for efficient photosynthesis below about 60 m (although modern cyanobacteria are known from greater depths!). By constraining the stratigraphic measurements Keupp obtained the following results: The Solnhofen–Langenaltheim basin is thought to have reached 50–60 m in depth, whilst the Eichstätt basin did not exceed 30 m. The Painten basin was also shallow with a maximum depth of 20–30 m, and the Kelheim basin is calculated to have reached 50 m.

STAGNATION OF THE BOTTOM WATERS

In the absence of circulation to these isolated hollows, the waters stagnated, developing their own local chemistry which is responsible for the exceptional preservation of the Solnhofen fossils. The peculiar composition of the waters not only deterred normal marine organisms from living in this environment, but for any organism unfortunate to be washed over the reef and steeped in this solution, death followed very shortly afterwards. Hence the examples of mass mortality and sudden death seen in some of the fossils (see palaeoecology, pp. 77–9, and taphonomy, pp. 89–90). Very few of the organisms were still alive by the time they reached the surface of the sediment and those animals which did survive are well known from other occurrences for their tolerance to extreme environmental conditions. For example, the juvenile horse shoe crab, *Mesolimulus* and the crustacean *Mecochirus* were still alive for a short time on the lagoon floor.

These creatures produced the famous spiralling trails with the body lying at the centre, interpreted as the last, disorientated crawl of an moribund animal before it collapsed in its tracks. Even though a few hardy species may have survived for a short time in the lagoon, most animals were killed quickly and

the bodies fell through the water to come to lie on the sediment surface. Normally corpses lying on the seafloor are not left undisturbed because they are utilized as a food source by scavenging animals. They would be dismembered and partially consumed, producing a large surface area for chemical degradation by microbes and eventually resulting in the recycling of the organic molecules for the growth and construction of other organisms. But this was not the case in the Solnhofen environment. The origin of the exceptional preservation of the Solnhofen fossils is linked to the exclusion of macrobenthos from the site of burial, which ensured that the bodies were not ripped to pieces. Furthermore, the inactivation of a large section of the normal microbial community resulted in a very slow rate of decay. Together these factors helped to ensure the remarkable preservation of the Solnhofen fossils.

Chemistry of the Solnhofen waters and special preservation

HYPERSALINITY?

The most convincing explanation for the poisonous properties of the stagnant waters, that so favoured the exceptional preservation of the fossils, appears to be an excessive concentration of salt. Regrettably, the evidence for hypersalinity continues to be indirect. On pp. 71–3, the evidence for the climate affecting the Solnhofen area is discussed. Arguments point to hot and dry conditions, with no indications of any substantial runoff from adjacent landmasses. Under such conditions, evaporation would be intense and, as the salinity increased, the dense brine would collect in pools at the bottom of the basins. The brine would have a range of consequences for the biota and its preservation. Because elevated salinities are fatal to most normal marine organisms, macrobenthos would be excluded from inhabiting the lagoon. These animals stop functioning in hypersaline solutions because water is withdrawn osmotically from the tissues. The shrivelled appearance of many Solnhofen jellyfish (especially those from the Gungolding–Pfalzpaint area) is quite consistent with this idea of hypersalinity. Another consequence of hypersalinity is the preservation of organic material. 'Pickling' in salt solutions is an effective method of culinary preservation, because many of the decomposing microbes are inactivated and the decay processes greatly slowed. In natural hypersaline environments there are documented cases of exceptionally slow organic decay which has resulted in special preservation of organisms. For example, in the extremely hot environment of Death Valley, California, there are examples of exquisite preservation of insects in the salt-rich sediment (W. Berger, pers. comm., 1989).

The analogy between these extremely salty environments and the Solnhofen lagoonal basins cannot be carried very far, because salt concentrations in the

Solnhofen waters never reached very high values and the evaporating lagoonal waters must have been constantly diluted by an influx of normal marine water. Certainly the salinity of the lagoonal waters nearly always remained below the level of saturation with respect to the common dissolved salts, as there are no evaporite beds in the plattenkalk sequences. This consideration limits the salinity in the bottom waters to a maximum of 117 ppt, which is the approximate salinity at which the first salt, gypsum ($CaSO_4.2H_2O$), would start to precipitate. Sometimes the traces of salt crystals, long since dissolved away and infilled by calcite (making salt pseudomorphs) are found on bedding planes, but they probably did not form on the lagoon floor and attest only to local conditions within the sediment.

A more revealing modern analogue to these salinity-stratified lagoonal basins could perhaps be the Orca basin, Gulf of Mexico (e.g. Trabant & Presley 1978). This lies in a hollow in the continental shelf under fairly deep water of about 1700 m (and in that it is very dissimilar to the relative shallow plattenkalk basins). A layer of brine has formed at the bottom of this depression as a result of the dissolution of some of the underlying evaporite deposits. During many centuries organic matter and other terrestrial sediments from the North American continent have been washed into the stagnating basin. Decaying organic matter has totally depleted the brine layer of oxygen. In the anoxic and hypersaline waters, nothing, apart from the microbial community, is able to survive, and without macrobenthic organisms to bioturbate the sediment, a fine lamination is preserved. The remains of dead planktonic organisms which fell into the basin, such as the tests of calcareous foraminifera and siliceous radiolarians, are exquisitely preserved. The occasional fragments of seaweed, which found their way into the sediment, show remarkable preservation in that the details of cell walls are still visible (Kennett & Penrose 1978).

In the Orca basin anoxicity is the most important factor in retarding the rate of decay and promoting exceptional preservation. Hypersalinity most likely has a secondary effect in inhibiting the action of the sulphate-reducing bacteria which are the first bacteria to oxidize organic matter under anoxic conditions. This is inferred from measurements of the activity of these bacteria which is abnormally low in comparison with those measurements from exclusively anoxic water such as the Black Sea (Wiesenberg *et al*. 1979).

ANOXICITY?

Anoxia has developed in the Orca basin not merely because it has been stagnant for a very long time (carbon 14 calculations give a value of 79 000 years), but also because it has a high organic input and is too deep for any *in situ* oxygen production by photosynthesis. Using the Orca basin as a broad analogue for the plattenkalk basins, we can examine the various factors upon which the oxygen content depends. After a storm-induced exchange with the

Tethys Ocean, the water body begins with a certain oxygen concentration, most probably approaching the maximum amount of dissolved oxygen which may be held in waters of normal marine salinity (5.4 ml/l at salinity 35 ppt and 18 °C, see fig. 4.2). During stagnation the oxygen concentration will fall on two accounts. Firstly, with degradation of organic matter oxygen is used faster than it can be produced photosynthetically in the lagoon. Secondly, it will fall slowly as the salinity of the water rises and is able to hold less oxygen in solution (see graph of salinity vs oxygen concentration, fig. 4.2). If a state of almost total anoxia in the bottom waters has been reached, the terrestrially derived organic matter is no longer broken down by aerobic microorganisms and accumulates in the sediment. (The presence of organic matter does not necessarily mean that the bottom waters were anoxic. If a large amount of organic material is buried in a rapidly accumulating sediment, pore waters become anoxic because they have lost contact with the overlying bottom waters, even though the latter may still be oxic). The Upper Solnhofen Plattenkalk does not, in general, have a high proportion of preserved organic carbon, compared to some other plattenkalks. Hückel (1974b) mentions a measurement of 0.2% total organic carbon (TOC) from a flinz bed and 0.9% TOC from a fäule bed. This contrasts with an average value of 1.2% for micritic limestones (while the very organic-rich plattenkalk of Hjoula in Lebanon reaches 2.4%). Certainly, the underlying beds (Lower Solnhofen Plattenkalk, malm zeta 2a at Eichstätt, and plattenkalk from the malm epsilon at Painten) and the overlying beds (Mörnsheim beds in the Solnhofen–Eichstätt region) are more organic rich. The organic matter imparts a brown–black rather than a grey–yellow colour to fresh surfaces and produces a sulphide smell on fracturing. The absence of preserved organic carbon is most likely indicative of a very low fallout of organic material to the sediment, in other words lagoonal productivity was negligible. Under these circumstances it is less likely that anoxia would be reached in the time available before mixing and exchange of the lagoonal waters.
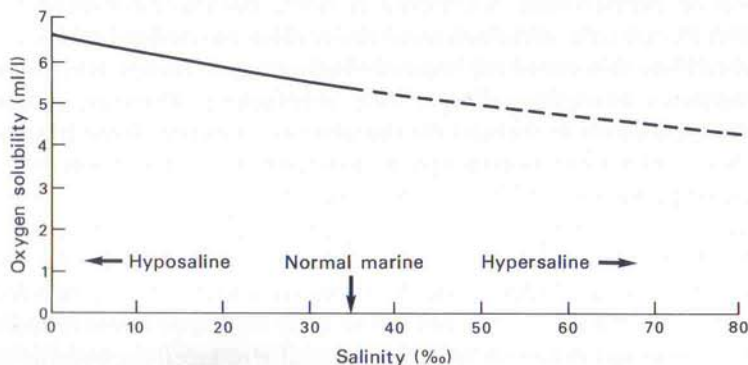

Fig. 4.2 Oxygen concentration in waters of varying salinity demonstrating how, with increasing salinity, oxygen solubility decreases. From Carpenter (1966).

Other arguments for a general oxicity of the plattenkalk waters have also been presented. Veizer (1977) measured the iron and manganese contents of calcium carbonate from the plattenkalk flinz beds and compared his results with those from other south German Jurassic deposits. The elements Fe and Mn were introduced into the plattenkalk sediment, bound inside the lattices of clay and oxide minerals, iron predominantly in the valency state III and manganese in IV. Under reducing conditions these elements gain electrons from other atoms and acquire a valency state of II. Fe^{2+} and Mn^{2+} are water-soluble ions and move out of their original minerals into solution. Accordingly, calcite which precipitated from anoxic waters would incorporate a relatively high content of soluble Fe and Mn, in relation to a calcite precipitated from oxic waters. Veizer obtained average values of 100 ppm Fe and 70 ppm Mn for the concentrations of these elements in the flinz carbonate. These results are consistent with values obtained from carbonates which formed in normal marine rather than those from anoxic environments. However, given the probable mode of deposition of these carbonates the results are perhaps not very surprising. If (as described on pp. 65–7), the flinz beds are made out of carbonate formed in normal marine environments, deposited rapidly and lithified early, then they should show a normal marine signature. To test if the bottom waters were anoxic the Fe and Mn contents of the well-preserved foraminifera (which presumably suffered very little diagenetic exchange) should be measured. As the foraminifera almost certainly lived in the lagoon we might then have a sounder basis for comment on the oxicity of the lagoonal waters.

The two other arguments generally cited in favour of low oxygen concentration in the plattenkalk waters we find similarly inconclusive. Firstly, there is the argument based on pyrite. Pyrite (FeS_2) forms under anoxic waters or in anoxic sediments. The sulphide ion is supplied by the bacterial reduction of sulphate, which is derived mainly from seawater and the Fe^{2+} from the reduction of Fe(III) minerals. Pyrite is not a common constituent of the Solnhofen Plattenkalk, although some finely disseminated pyrite does cause a blue–green tinge to some of the Solnhofen lithographic stones. But in comparison with known anoxic deposits it is noticeably lacking. There are a number of possible explanations to account for the absence of pyrite, some of which can be dismissed. The suggestion that pyrite formed but has since been redissolved is addressed by Keupp (1977a, b). He argues that this is not the case, because there are no 'etching' structures on the calcite particles which would be made by an acidic solution which dissolved the pyrite. An explanation for the non-formation of iron sulphides could be in the inactivity of sulphate-reducing bacteria because they are inhibited in the salty waters or because the waters were not anoxic and other bacteria preferentially reduced the organic matter. One of many other explanations is a deficiency of iron, because the supply of iron-containing minerals was too low.

A final argument advanced concerning the oxicity of the bottom waters is based upon the preservation of the siphuncle of ammonites. The siphuncular tube is a paper-thin, weakly phosphatic structure which runs inside the margin of the ammonite shell to the initial chamber from which the animal commenced growth. In black shales deposited under anoxic conditions, although the specimens are crushed, the siphuncle is preserved as a distinct dark-coloured line. Siphuncle preservation is normal for ammonites in the Mörnsheim beds overlying the Solnhofen Plattenkalk but, according to Keupp (1977a, b), the siphuncle in the plattenkalk ammonites is not preserved and this is evidence against widespread bottom water anoxicity. Others, notably G. Viohl of the Jura-Museum, Eichstätt, would disagree with this statement of Keupp's, claiming that siphuncle preservation in the plattenkalk ammonites is not uncommon and making redundant this argument for plattenkalk water oxicity.

In all probability, oxygen concentrations varied from normal marine to almost anoxic, this depending upon the period of salinity stratification and the resultant degree of stagnation.

OTHER POSSIBILITIES?

A different explanation of the hostile conditions prevalent in the lagoonal waters was put forward by Paul de Buisonjé of Amsterdam (1972, 1985). de Buisonjé proposed that an upwelling current (presumably off the shelf edge) produced seasonal blooms of coccolithophorids in the lagoonal waters. As these microorganisms died and fell through the water column, toxins produced in the decay of their bodies soon poisoned the bottom waters. Upwelling mixed this putrid water throughout the entire lagoon ensuring an environment hostile to any marine macroorganisms which the currents had swept into the area. Their corpses sank to the bottom to be buried by a rain of coccoliths from the overlying waters.

de Buisonjé's speculations are based on what appear to be very insecure premises. The original idea that the plattenkalk 'lagoon' was subject to an upwelling current is clearly based on the superficial similarity between palaeo-geographic reconstructions of the plattenkalk lagoon and 'semi-enclosed marine basins which have their long axes more or less parallel to the direction of the wind and open downwind' (de Buisonjé 1985). As discussed on p. 71, the Solnhofen area most probably lay in the zone of the trade winds running ENE–WSW, but there are no direct indications of any water or wind current directions available from the Solnhofen–Eichstätt area (those he cites are local directions of palaeoslope, see p. 34). Unfortunately, we simply do not have enough information to constrain the orientation of the basin, especially as the position of land on the palaeogeographic map is only inferred from negative evidence, and in any event upwelling within the lagoon itself seems unlikely.

A major objection to de Buisonjé's theory concerns his suggestion of high

productivity in the surface waters of the lagoon, a consequence of the upwelling current. Where then are the numbers of nektonic macroorganisms which fed off this plankton and which we would expect to be embedded in the sediment, particularly the fäule sediment? The scarcity of fossils from the Solnhofen limestone indicates the essential sterility of the lagoon. As present-day coccolithophorids have never been shown to produce measurable quantities of toxins in their decay, there seems to be no reason to suppose that the decaying coccolithophorids in the Solnhofen lagoon would poison the water. de Buisonjé then suggested that other plankton which bloomed with the coccoliths, such as the dinoflagellates, were the toxin producers, but that they were not preserved, which makes this idea difficult to test further. In addition, and perhaps most conclusively, the very low concentration of organic matter in the plattenkalk also indicates that the lagoon was an area of low productivity.

Blooms of microorganisms

As hypersalinity never achieved the high values leading to the precipitation of evaporites, the stagnation can only have been temporary. The water column mixed and exchanged with the open sea, diluting the overall salinity and refreshing the lagoonal waters. Immediately after these episodes, conditions were sufficiently equitable, especially with regard to oxygen, to allow certain opportunistic species of microorganisms, mainly benthic foraminifera and coccolithophorids, to complete their short life cycles in the lagoon. The protists matured and reproduced before the salinity became too high for their continued survival, and their tests collected on the surface of the sediment.

During formation of these microfossil laminae (thin intercalations between flinz beds and in fäule interbeds) the salinity must have been less than 60 ppt (C. Hemleben, pers. comm. 1986) even at the bottom of the lagoon to permit foraminiferal growth, and yet must have been sufficiently high so that macrobenthos did not enter the lagoon and bioturbate the sediment. Salinities of 40–50 ppt would be quite sufficient to deter most animal and plant species (Hemleben 1977) and both the assemblages of coccoliths and foraminifera are consistent with the idea of weak hypersalinity throughout the water column at these times (see palaeoecology, pp. 73–4).

The cyanobacterial mat

The fäule and possibly to a lesser extent the flinz have yielded the coccoid spheres thought to be the remains of cyanobacteria (see pp. 45–7), and their occurrence fits well into the environmental reconstruction so far presented. As salinities increased to levels which the protists could not tolerate, one of the few

organisms left to inhabit the otherwise sterile environment were the cyanobacteria. Cyanobacteria still flourish under very salty water, forming a mat on the surface of the sediment which is not disrupted by burrowing organisms. Consolidated by the slime produced by the cyanobacteria, the mat surface is further hardened to a thin surface crust by the calcium carbonate which precipitates around the cells as a by-product of respiration.

This enveloping of the limy sediment by the cyanobacterial mat resulted in a cohesive texture to the surface of the sediment (rather than the 'soupy' texture which is found in lime muds of modern carbonate environments), ideal to take up the delicate traces made by the Solnhofen organisms. A cyanobacterial mat which grows over corpses lying on the sediment surface, encapsulating them in a film of calcium carbonate, could help to explain the unusual nature of the preservation. Modern cyanobacterial mats will grow over entire corpses within hours or at most days (D. Herm, Munich, cited by Keupp 1977a). An impression of the body is taken up into this thin calcareous mould before internal decay sets in and the corpse falls apart. Within the strongly reducing environment created inside this calcareous envelope, the soft tissue decays extremely slowly and the body resists the pressure of the surrounding sediment for a relatively long time. When the body finally collapses, the surrounding sediment is already quite well consolidated and this gives rise to the characteristic pedestal preservation of the Solnhofen soft-bodied fossils (see fossil diagenesis, pp. 96–9). Preservation of the fossils by the cyanobacterial mat seems entirely plausible, but if Barthel's depositional theory is followed rigorously there is not time for growth of a cyanobacterial mat before the sediment (which arrived in the lagoon in the same current of water) settled over the corpses. It seems that a cyanobacterial mat may well have been present in this type of environment (and see later under deposition) but it is not necessarily responsible for the preservation of the fossils.

A depositional model

The general consensus, promoted by Barthel, regarded the plattenkalk sediment as a carbonate ooze which had accumulated around the coral reefs (fig. 4.3). Periodically, storms stirred up this sediment from the seafloor and it became suspended in the turbulent water (fig. 4.3b). The sediment-laden water washed over the coral patch reefs and flooded into the lagoon, the coarser fraction of the sediment, the 'reefal debris', being dropped after a short distance, whilst only the finest particles were transported the long distance to the Solnhofen area. Some reefal organisms were also drawn into the lagoonal waters. Their bodies sank to the lagoon floor to be covered by the more slowly settling, finer sediment (fig. 4.3c).

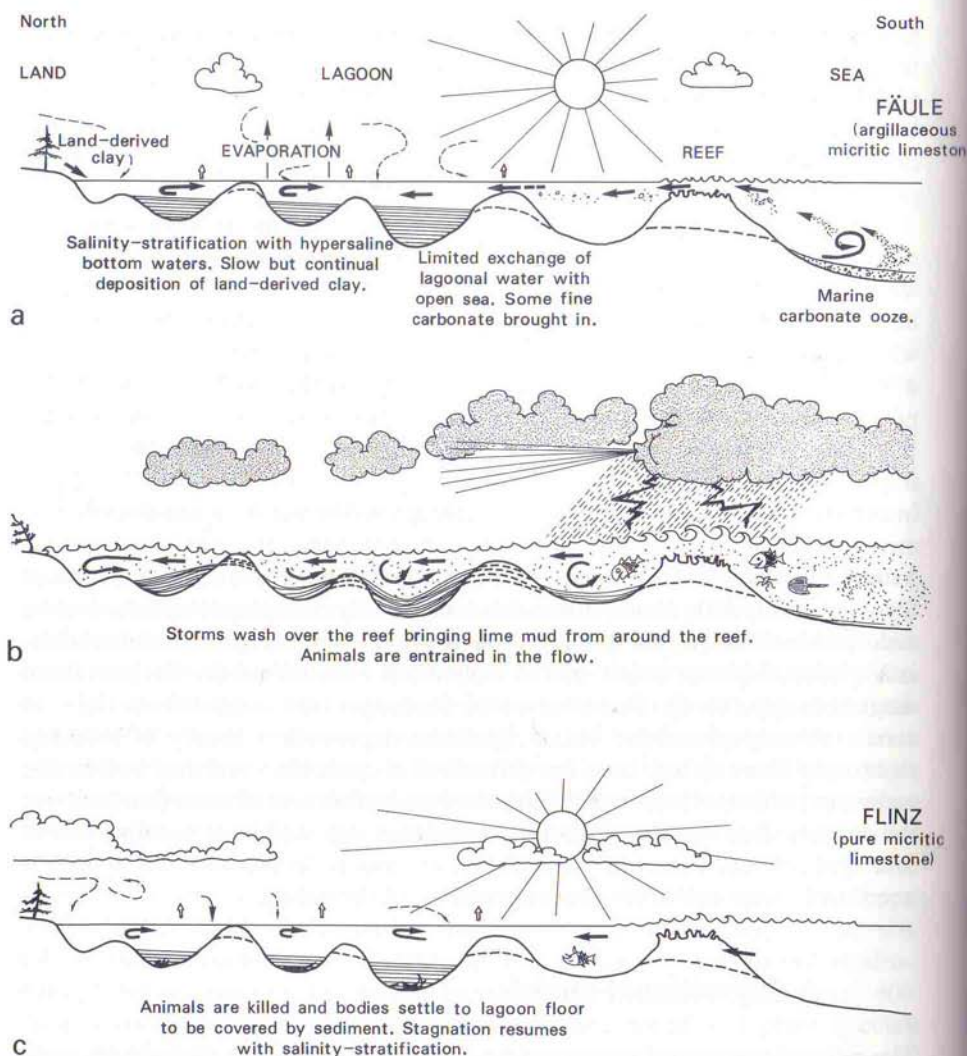This 'suspension theory' of sediment transport was first propounded by the

Fig. 4.3 Barthel's theory of deposition of the Solnhofen Plattenkalk. The carbonate in both flinz and fäule is regarded as allochthonous and of shallow marine origin.

Dutch sedimentologist van Straaten (1971). Deposition out of suspension explains how the particles rained down vertically upon the dead organisms and shells. The different pulses of sediment each formed a lamina draping around the fossil. This is an unusual phenomenon; usually potential fossils are buried by a unidirectional, sediment-laden current which will smooth the sediment surface over the site of burial. In contrast, the deposition of the plattenkalk was

not accompanied by currents over the basin floor. In the Solnhofen–Eichstätt area this is clearly shown by the saucer-shaped *Inoceramus* and *Ostrea* shells and ammonite aptychi, 90% of which lie convex down, in an orientation unstable in currents. Some bulbous ammonite shells such as *Aspidoceras* and the occasional belemnite are embedded vertically in the sediment and this is the position in which they would first have settled. Other indications of very quiet water are the resting impressions found adjacent to the body fossils formed as the sinking animal touched down. The blanket cover of fine sediment also provides an explanation for the correlation of beds for many kilometres within some basins (correlation of flinz beds between different basins being a little more problematic).

Barthel saw no essential difference between deposition of flinz and fäule. The flinz was a concentrated deposit brought into the lagoon by the stronger storms, whilst the fäule carbonate drifted in on gentle currents (too weak to entrain animal bodies), accumulating slowly over a long period of time and diluted by land-derived clay (fig. 4.3a). The now well-preserved coccoliths and benthic foraminifera, which (according to Barthel) form only a small percentage of the fäule carbonate, grew in the lagoon at times when the lagoonal waters (which were never in complete isolation from the sea) were of lowest salinity. Barthel also suggested that the foraminifera might have grown on the sides of the sponge–algal mounds and been washed into the more hypersaline depths.

The time taken to deposit a flinz/fäule couplet can be estimated only extremely roughly and by the following calculations: the amount of ammonite evolution between the top and bottom of the Solnhofen Plattenkalk is equivalent to about half an ammonite zone and, in Upper Jurassic rocks, one ammonite zone must last for on average a million years (given the number of ammonite zones and the total time to deposit the Upper Jurassic rocks as calculated from radiometric dates). Therefore, the Solnhofen Plattenkalk (Upper + Lower) may have taken around 500 000 years to be deposited. In this time some 500–2500 flinz/fäule couplets were formed (as calculated by the average thickness of the beds and maximum thickness of the sequence), so that, on average, each flinz + fäule cycle took of the order of 200–1000 years to be deposited.

Other depositional theories

Whilst accepting that the flinz sediment was allochthonous (i.e. brought into the lagoon), rather than autochthonous (formed in the lagoon), Adolf Seilacher (Seilacher 1963, Goldring & Seilacher 1971) thought that the flinz beds were the end products of turbid flows of lime mud down the sides of the sponge–algal mounds. This is almost certainly the case for other plattenkalks,

many of which show clear evidence in the form of grading, basal gouge and scour marks and beds of limited areal extent. However, most other authors reject the suggestion that the plattenkalk beds are turbidites on the following grounds. If the individual plattenkalk beds have been correctly correlated between outcrops and are thus single episodes of deposition, then it seems difficult to see how a single turbidity current could be responsible, given the highly irregular topography of the lagoon floor. It is certainly true that some of the plattenkalk beds are graded, but deposition of any suspended sediment can produce this. There are also a few examples of ammonite rollmarks from the Solnhofen–Eichstätt area. According to Seilacher these must have been produced by ammonites being bowled along the surface in a strong, sediment-laden flow, and are inexplicable in a gentle energy regime. But, according to Viohl (pers. comm. 1986), the rollmarks cited by Seilacher are not from the Solnhofen Plattenkalk at all, but from the Mörnsheim beds, which were deposited under quite different conditions. Nevertheless, some beds in the Painten area are definitely turbidites. These obviously graded beds, where ammonite rollmarks and other scratch marks are common, wedge out over distances of tens of metres. It is also quite likely that some of the flinz beds from Solnhofen itself may have thickened by slippage of sediment down the sides of the sponge–algal mounds.

Another variant on Barthel's depositional theory was provided by Hemleben (1977), who also considered the flinz to be an allochthonous marine ooze, but thought that the bulk of the fäule carbonate was autochthonous and made of lagoonally produced coccoliths and benthic foraminifera. In postulating that during intervals of fäule accumulation, biological production in the lagoon extended from the surface right down to the lagoon floor, Hemleben then had to dispense with the idea of hypersalinity as the supposed explanation for exclusion of macrobenthos. As a substitute he suggested that the sediment texture was too soupy for macrobenthic colonization, but this does not explain the rarity of macropelagic fossils in the fäule.

Based on his own observations and recognition of cyanobacterial spheres in the fäule and flinz (see pp. 44–8), Keupp's (1977a, b) depositional model is ingenious and fundamentally different to Barthel's. Under Keupp's theory the flinz was produced on the lagoon floor under stagnant, salty water of varying oxicity by the uninterrupted activities of cyanobacteria (see fig. 4.4). From time to time the surface waters would be mixed by turbulence and would exchange with normal seawater, so refreshing the upper layers of the lagoon. During these brief periods coccolithophorids were able to grow in the upper waters. On death they fell to the lagoon floor and now constitute the distinct white coccolith laminae in the flinz. Clayey bedding planes formed when the entire water column mixed, killing the cyanobacterial mat, temporarily halting the carbonate production and resulting in a relatively higher clay content for the lamina (there is continual background deposition of a marine clay). The waters
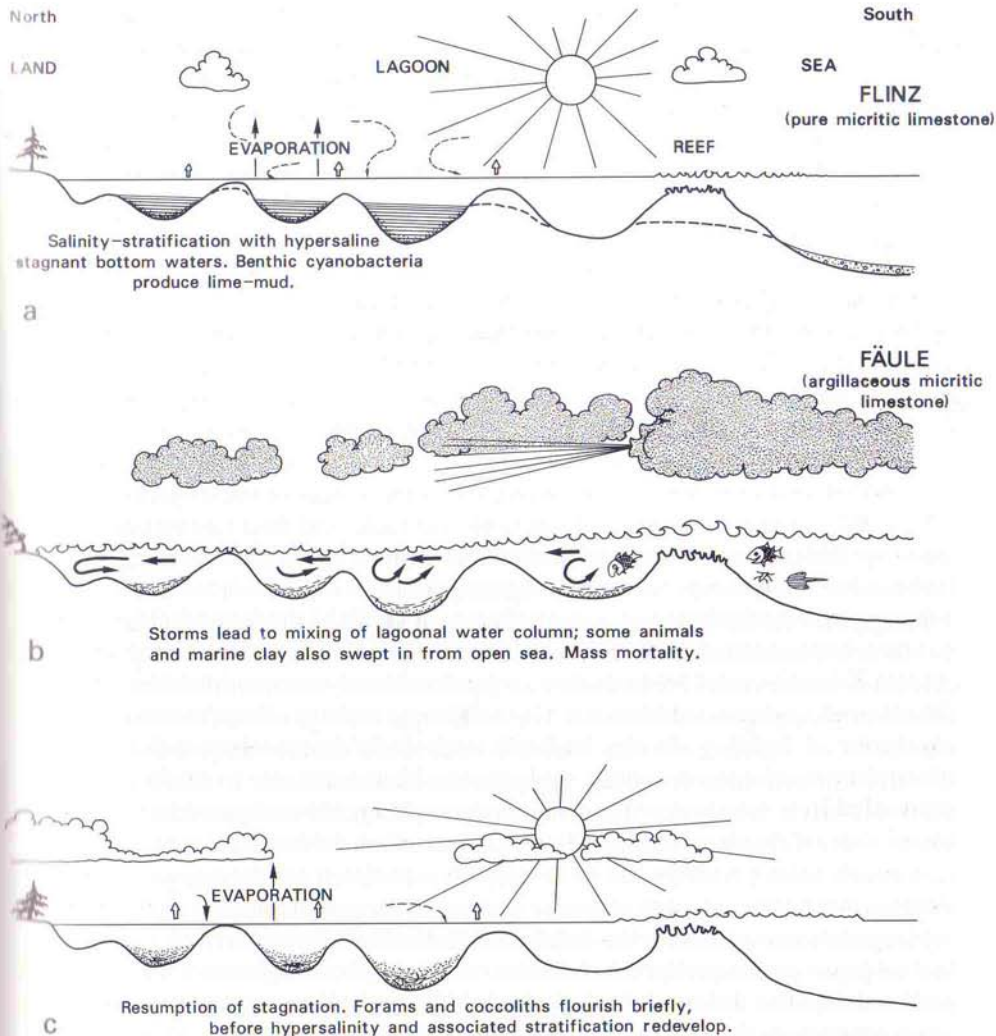
Fig. 4.4 Keupp's theory of deposition of the Solnhofen Plattenkalk. The flinz and some of the fäule carbonate is autochthonous and precipitated due to the activities of cyanobacteria which grew on the lagoon floor. Fäule is formed by a repeated mixing of the entire lagoonal water column. The lower calcium carbonate production by the cyanobacteria over this period is responsible for the relatively higher clay content of the bed. Cyanobacteria produce calcium carbonate continually when a flinz bed is made. Any mixing is restricted to the top of the water column, refreshing only the surface waters and allowing coccolithophorids to grow and be deposited in the flinz sediment.

mixed and exchanged with the open sea, bringing into the lagoon a sparse macrobiota, which was predominantly nektonic. Most of these animals were killed on contact with the salty water and their bodies came to lie in the thin shaly lamina. With further water exchange planktonic coccolithophorids began to inhabit the surface waters together with the nektonic animals which fed off them which produced the coprolitic pellets. With the return of stagnation the foraminifera were unable to survive and the lagoon floor was again taken over by the cyanobacteria.

For Keupp, the fäule consists of a stack of closely spaced clayey coccolith/ foraminiferal laminae intercalated between thin cyanobacterial laminae (see fig. 3.8, p. 48). Thus fäule production represents repeated events of holomixis (mixing of the entire water column) between briefer periods of stagnation. The cyanobacterial laminae which make up the bulk of the flinz are seen as identical in composition to those in the fäule but more diagenetically altered. Flinz cyanobacterial carbonate is interrupted by intercalated coccolith-rich laminae which represent short periods of mixing and refreshment of the surface waters during the general stagnation. Thus both the fäule and flinz laminations are seen by Keupp as primary sedimentary rhythms (although others, such as Hemleben, see these as primarily diagenetic).

Keupp has certainly made a more thorough study of the microfacies of the Solnhofen Plattenkalk than any other investigator and so his views deserve careful consideration. Nevertheless, a predominantly stromatolitic origin for the flinz seems questionable for the following reasons. First, consider the regularity in bedding. In the Eichstätt area beds are continuous for many kilometres, and almost never wedge out. Moreover, on a smaller scale, the millimetric lamination is planar and not irregular and wrinkled. These features are difficult to reconcile with stromatolites (although it is true to say that stromatolites which grow at the depths postulated for the lagoon are not well studied). The absence of pyrite and very low concentration of preserved organic matter suggest that the Solnhofen Plattenkalk formed in waters of very low organic productivity. In contrast, most algal mats have a very high productivity; the sediment becomes sulphidic and organic matter is in most cases preserved. So it is quite conceivable that the cavities in the fäule are of cyanobacterial origin, but it may not be an automatic consequence that they were important in generation of the flinz.

5   Palaeoecology

Palaeoclimate

Palaeogeographic reconstructions for the Late Jurassic world show southern Germany and so the Solnhofen district to be somewhere between latitudes 25° and 30° N. In this latitudinal belt, albeit on a globe with somewhat different distribution of continental masses, we can infer that the Solnhofen area would have lain in the subtropical, semi-arid zone. This region would have been subjected to seasonally wet winters and prolonged dry summers, but as mountain ranges were absent in the region, overall there would have been little rain.

The general indications are of a warm, but desiccated climate. The first line of evidence for this comes from the general sedimentology. Limestones are the predominant lithology of the Upper Jurassic strata of southern Germany, and although carbonates can form under cold climates, they predominate in warm waters where there is a wealth of calcareous shell-forming organisms. The Solnhofen carbonate is also unpolluted by terrestrial sediment, so it seems unlikely that major rivers washed off the land into the lagoon. In turn, this suggests a lack of rainfall and an arid climate. The types of animals and plants present also support this conclusion. In the subtropical climate coral reefs flourished in the Southern Franconian Alb. The corals in these Jurassic reefs may not be identical to today's forms, but they are sufficiently similar for us to suppose that they lived in clear, warm water, probably in the range of 20–30 °C. A temperature value of 26 °C for surface water temperature was obtained by analyses of the oxygen isotopes in two calcitic belemnite guards (Engst 1961). This method of palaeotemperature calculation relies on the observation that ratio of different isotopes of oxygen ^{18}O and ^{16}O incorporated into calcite depends on the temperature of the seawater in which it forms as well as its latitude, salinity and several other complicating factors. The value for water temperature is calculated using the Epstein formula:

$$T(°C) = 16.9 - 4.2(\delta_c - \delta_w) + 0.13(\delta_c - \delta_w)^2$$
where:
$\delta_c = \delta^{18}O$ of CO_2 generated from carbonate at 25 °C (relative to a belemnite from the Pee Dee formation in South Carolina, USA)
$\delta_w = \delta^{18}O$ of CO_2 generated in equilibrium with water at 25 °C (relative to Standard Mean Ocean Water (SMOW))

From Epstein *et al.* 1953

The temperature on land would have been higher still, and intense evaporation exceeded the small amount of precipitation. The plants now fossilized in the Solnhofen Plattenkalk exhibit various adaptations that seem to reflect the need to cope with water shortage (e.g. Meyer 1974). The seed fern *Cycadopteris* reduced evaporative water loss by a thick leathery cuticle which covered the upper surface of the leaf and also overhung the sides as rims. Moreover, the stomata of the plant which were restricted to the underside of the leaf occupied sunken pits. The conifers *Brachyphyllum* and *Palaeocyparis* had tough cuticles and minimized the exposed surface area by adopting scale-like leaves. These plants were strengthened by a central rod of wood, surrounded by an outer cylinder of spongy pith tissue (now calcified) in which the plants could store a certain amount of water (Jung 1974b). Similar structures are found in the present-day cactus where the pith cavity is an adaptation to a dry climate. Another incidental consequence of this construction is that the conifer stems could never have grown to any substantial height (less than 3 m) because of the relative weakness of the slender stems.

Weathering of land under a hot, dry climate yields characteristic products. In the chemical weathering of silicate-containing rocks to clay minerals, the proportion of the clay kaolinite relative to montmorillonite and illite can be influenced by climate. Generally kaolinite forms in more acidic milieu and particularly in hot and humid conditions, but it is important to realize that many other factors also control clay mineral distribution. In practice, so much depends on the composition of the parent rock and the chemistry of the depositional environment that the palaeoclimate was probably of secondary importance. In the Solnhofen Plattenkalk, there is a low but variable amount of kaolinite with respect to illite and montmorillonite (e.g. Hückel 1974a) and considerably less than in the beds either immediately above or below. The Solnhofen Plattenkalk is also anomalous in the complete disappearance of illite in favour of mixed layer minerals. All this seems to suggest that the platten-kalk's depositional environment was unusual, but in what respect, the clay minerals do not easily tell us.

The fine clay fraction in the plattenkalk sediment was probably carried into the lagoon by wind rather than water. The few quartz grains show clear evidence of aeolian transport in that when examined under the electron microscope they are spherical and have frosted surfaces. Although this does not necessarily exclude a final period of water-borne transport into the lagoon, there is no direct evidence for the presence of major rivers emptying into the lagoon. Neither channels nor associated sedimentary structures typical of fluvial environments are found and the lagoon was essentially starved of terrigenous sediment. However, the few bodies of land animals and plants must have been transported somehow into the lagoonal sediments and,

spasmodically, rivers must have drained the land surface. Freshwater ponds must also have existed seasonally on the land to provide a home for the larval stages of the Solnhofen insects.

Life in the lagoon

Between the low-lying land to the north and the southern coral reefs, the lagoon itself presented a range of environments potentially open to colonization. Mounds, made from sponges and cyanobacteria (now dead) and their trapped sediment, protruded from the lagoon floor, leaving depressions where the plattenkalk sediments accumulated. The irregular topography formed by the dead sponge–algal and coral-encrusted mounds would have helped to limit the strength of water currents. As the water stagnated, evaporation produced a salinity stratification through the water column with denser, hypersaline (and only weakly oxic, see pp. 60–3) water at the bottom of the basins. The density–salinity stratification was very stable. Weak water currents failed to remove the stagnant bottom waters and only the occasional, major storm could flush the waters from these hollows so preventing extremes of hypersalinity and evaporite precipitation. The storms also brought water laden with detrital particles of $CaCO_3$ into the lagoon from the reefal area and the open sea, and this sediment settled to form a soft, organic-poor ooze at the bottom of the basins.

The essentially sterile, benthic environment was hardly suitable for animals who were in search of either a food source or a home. It seems that food supply would have been very low. Little organic matter entered the lagoon from the open sea because of the various barriers to seawater circulation, and even less came from the surrounding land which was semi-arid and highly oxidizing so that most organic material would have quickly been recycled. Organic productivity in the lagoon itself was also very low because the hypersalinity excluded a normal marine biota. Scavenging organisms rarely entered the lagoon (although there are a few known examples of predation, see below) and the occasional corpse washed into the lagoon was left untouched. The sediment was uninhabited and therefore unbioturbated and undisturbed.

Often the sole occupants of such hypersaline environments are the cyanobacteria and these were almost certainly present in the Solnhofen lagoon. Hollow spheres, which were probably once occupied by coccoid cyanobacteria, are found in the fäule (Keupp 1977a, b, see pp. 45–7) and a surface cyanobacterial mat may have helped to bind together the carbonate ooze. When the mat decayed it could have provided nutrients which nourished a restricted population of ostracods and foraminifera. These invaded the lagoon floor during periods of slight water-mixing and refreshment of the bottom waters. The assemblage of foraminifera is impoverished in terms of numbers as well as

species and consists almost entirely of smooth, unornamented forms (Groiss 1967). This is clearly indicative of hostile conditions which only a few forms could tolerate. Groiss (cited in Viohl 1985) also asserted that the foraminiferal abundance and diversity decreased from Eichstätt towards Solnhofen and Langenaltheim, and this may be in a direction of increasing water depth and more permanent salinity stratification. Ostracods from Langenaltheim, studied by Gocht (1973), were not preserved in sufficient detail to allow them to be identified even to the level of genus so, despite their general utility in palaeoenvironmental reconstructions, they cannot help in any discussion as to the salinity. But the ostracods were not immune to the hostile environment and their death seems to have been sudden. Thus, they are preserved in life position with the bivalved shells vertically embedded in the sediment before they were subsequently squashed during sediment compaction.

Accompanying the foraminifera and occasional ostracods on these clayey surfaces are a scattering of coccoliths, the remains of coccolithophorids which would have lived in the surface waters of the lagoon. Some laminae contain quite diverse assemblages which may reflect normal marine conditions. Others are very poor, with a predominance of one species, *Cyclagelosphaera margereli*, which was presumably tolerant to conditions of increased salinity (Keupp 1978). Some coccoliths are preserved in intact coccospheres which would normally disaggregate only hours after the death of the algal cell which made them and so can only have been transported a short distance to their site of burial. One way to remove coccoliths rapidly from the surface into the conserving milieu of the bottom waters is inside the faeces of macroorganisms, as seems to have been the case for some of the fäule coccoliths.

Some macroorganisms may have existed for short times in the lagoonal waters. In particular, the small crinoid *Saccocoma*, which is found in large numbers at the base of some flinz beds, flourished on favourable occasions in the upper waters of the lagoon. Plates of *Saccocoma* can also be identified inside specimens of the worm-like faeces, known as *Lumbricaria intestinum* (Janicke 1970a). *Lumbricaria* is a contorted, worm-like tube with a circular cross-section (diameter 1–4 mm) and a length that may reach 170 cm (fig. 5.1). The fossil is made almost completely of calcite, mostly recrystallized but occasionally still showing the net-like reticulate fabric typical of echinoderm plates. *Lumbricaria* is one of the most common fossils in the Solnhofen limestone, and we might reasonably expect it to have been made by an organism represented in the commonest groups of body fossils, such as the fish, crustaceans or cephalopods. Squids and cuttlefish turn out to be the best candidates, because there are close comparisons between *Lumbricaria* and the faeces of the modern octopus (Janicke 1970a). The diet of these cephalopods must have included large numbers of *Saccocoma*, and the indigestible skeletal plates passed out in the faeces. Although the plates were probably bound together by mucus, the shape of *Lumbricaria* looks very much as if it fell
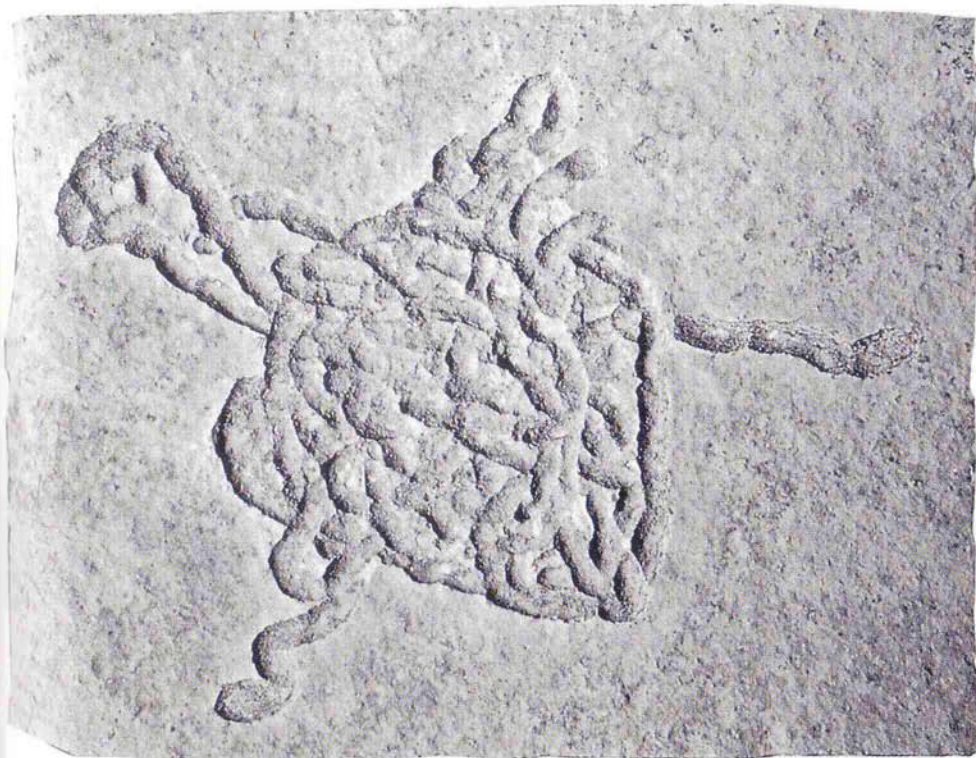
Fig. 5.1 Trace fossil; *Lumbricaria intestinum* Goldfuss, Schernfeld bei Eichstätt; maximum diameter of fossil 102 mm; BSPHGM 1964 XXIII 161.

directly from an organism which lived in the lagoon rather than being brought in from elsewhere.

A rarer type of *Lumbricaria*, referred to as a separate trace fossil species, *L. recta*, probably has a different origin. *L. recta* is an elongate worm-like trace shorter than the more common form, generally straight or slightly curved and preserved wholly or partly in a phosphatic material, sometimes accompanied by calcite (fig. 5.2). The phosphatic preservation suggests the coprolite consisted mainly of fish fragments with a secondary echinoderm component. The fragments which it contains are relatively large and presumably incompletely chewed. This, together with its short length, suggests its maker was probably a fish. Cough balls (Janicke 1970b) are another type of ejecta, but spat out of the mouth of an animal. An elliptical ball, 12.5 by 15 cm, which contained the scarcely chewed or digested remnants of a 45–50 cm long fish is shown in fig. 5.3. The distasteful morsel must have been regurgitated by a much larger fish or reptile. There are plenty of candidates for its maker, all several metres in length, in particular pachycormid fish or else some of the crocodilian reptiles.

Fig. 5.2   Trace fossil; *Lumbricaria recta* Goldfuss, Langenaltheim; maximum width of specimen 145 mm; collection, preparation and photograph Captain G. Brassel, Flensburg-Mürwik.

Very occasionally the Solnhofen fossils show signs of predation. Examples are crunched ammonite shells or half-eaten fishes without signs of decay (Mayr 1967).

The surface waters also carried the planktonic larvae of macroorganisms, in particular, bivalves. Some bivalve larvae found relatively stable sites for colonization in objects floating in the lagoon. When the bivalves grew too heavy for their float the entire assemblage sank to the bottom, quickly killing the bivalves. The associations of hosts with their encrusting partners are preserved together (fig. 5.4). The bivalves are juveniles of very similar size, mostly with the valves still articulated and attached to the host. Most are oysters of the genus *Ostrea* and, more occasionally, *Inoceramus*. They are found attached to certain gas-chambered cephalopod shells, such as ammonite conchs and belemnite rostra (but not the guard), as well as pelagic crinoids and probable algal fronds. Often the floats are quite large with several belemnites and ammonites (Seilacher *et al.* 1985). Some accumulations of small bivalves have no obvious carrier. They must have attached themselves to drifting bits of seaweed which are no longer preserved. Serpulid worms and lepadomorph barnacles also encrust some Solnhofen ammonites.

In most cases when marine organisms were introduced into the salty lagoonal

Fig. 5.3   Regurgitated *Caturus* (*Strobilodus*) sp., Blumenberg bei Eichstätt; maximum diameter 157 mm; BSPHGM 1964 XXIII 111.

basins the severe trauma was overwhelming and led to rapid death, probably before they reached the sediment surface. The sudden death of the organisms can be seen in some of the other fossil specimens. Some fish had evidently just had the benefit of a meal as recently eaten prey can still be seen in their stomachs. Even more astonishing are those fish with prey still in their mouths. These creatures evidently made a last snatch at a dying fish before they themselves perished (they also could have died from choking).

A very few, relatively tolerant animals were able to survive the hypersaline milieu for a short time, perhaps a matter of hours, but all their traces end in the

Fig. 5.4 The brown alga, *Phyllothallus latifrons* Rothpletz encrusted by oysters, Haunsfeld bei Mörnsheim; maximum extent of seaweed 185 mm, PAMNHUB.
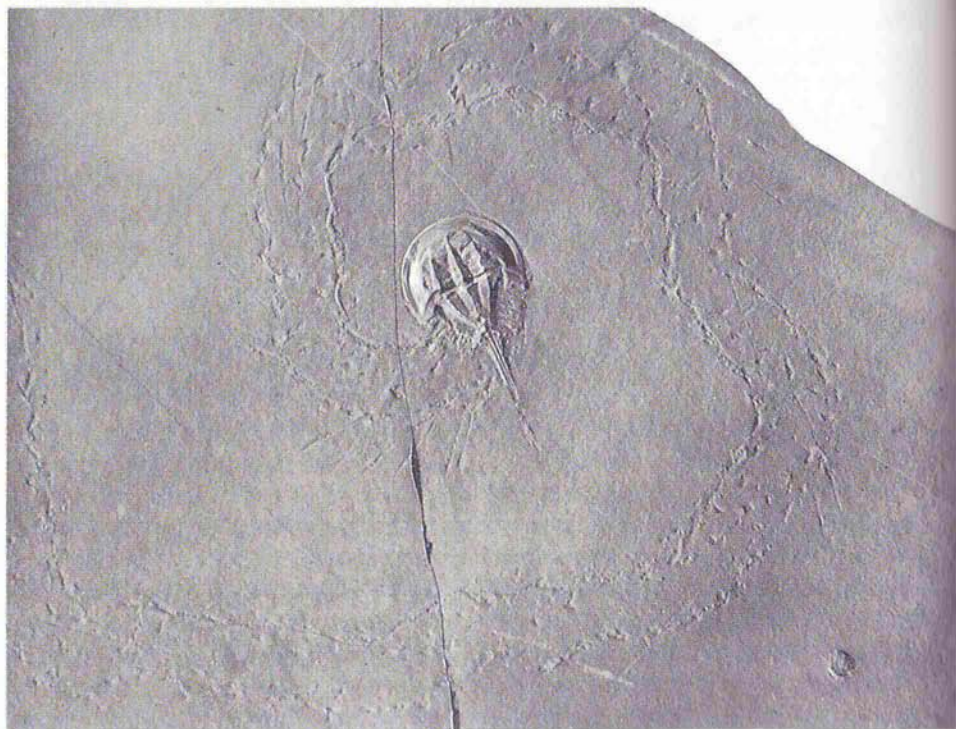
Fig. 5.5 Xiphosuran chelicerate; *Mesolimulus walchi* Desmarest and its spiral 'death' track, Maxberg bei Solnhofen; carapace width 92 mm; MSAV.

death of the beast. Washed into the stagnant, salty basin, they were merely able to crawl in a disoriented spiral before collapsing in their tracks. Most famous and comparatively common are the tracks of the horse-shoe crab, *Mesolimulus* (figs. 5.5, 5.6 & 5.7). The individuals which crawled and died on the plattenkalk sediment in the Solnhofen–Eichstätt area are all juveniles. More normal life activities of the larger mature limulids are found near to Painten, where the water was better mixed and comparatively more hospitable. In modern *Limulus*, juveniles, unlike adults, swim upwards when disturbed and so were probably more susceptible to being washed away. Of the juveniles' tracks recorded in the Solnhofen Plattenkalk one type of trace starts as the animal, which swims on its back (as do modern limulids), lands, turns itself over, and then goes for a short meandering walk (Fisher 1975a). The other type of trace is the spiral death track with the body at the end. It has been suggested that these represented moulting activity but this cannot be the case as there are no marks made by the animal after it had crawled out of its skin. Some of the longest of the spiral tracks were made by the bivalve *Solemya*, a genus well known for its environmental tolerance. Its muscular foot excavated a deep furrow in the sediment, the two edges of the gaping shell carving the outer furrows (figs. 5.8 & 5.9). Also known are shorter, irregular trails made by the gastropod *Rissoa* (figs. 5.10 & 5.11), which may be very numerous in places (particularly Pfalzpaint where the trails come from one or two beds, G. Viohl, pers. comm. 1988). *Rissoa* may have lived on strands of algae which were also carried into the lagoon marooning their passengers. Other tracks produced by the motion of a live animal across the lagoon floor were made by the shrimp *Mecochirus* (fig. 5.12, see also fig. 7.25). The shrimp seems to have jack-knifed backwards levering itself up by the tail and dragging its very long forelegs behind it.

Reefal communities

It is mainly the bodies of marine rather than terrestrial organisms which were transported into the plattenkalk basins and became fossilized. Some of these may have lived around the tops of the sponge–algal mounds which penetrated the less salty waters of the lagoon. Others must have come from communities on the periphery of the lagoon, either sponge-dominated mounds or else sponge–algal mounds overgrown by corals (see also stratigraphy, pp. 24–37). When the storms washed the organisms from these areas, some organisms were more likely to be carried away than others (see taphonomy, next chapter). This bias in the types of animals represented in collections must be borne in mind when piecing together the components of this Late Jurassic ecosystem.

Whilst sponges grew in thickets, trapping sediment between them and forming gently rolling mounds, the corals built a strong, steep framework. Some of these organisms, such as the calcareous bryozoans and (questionable)
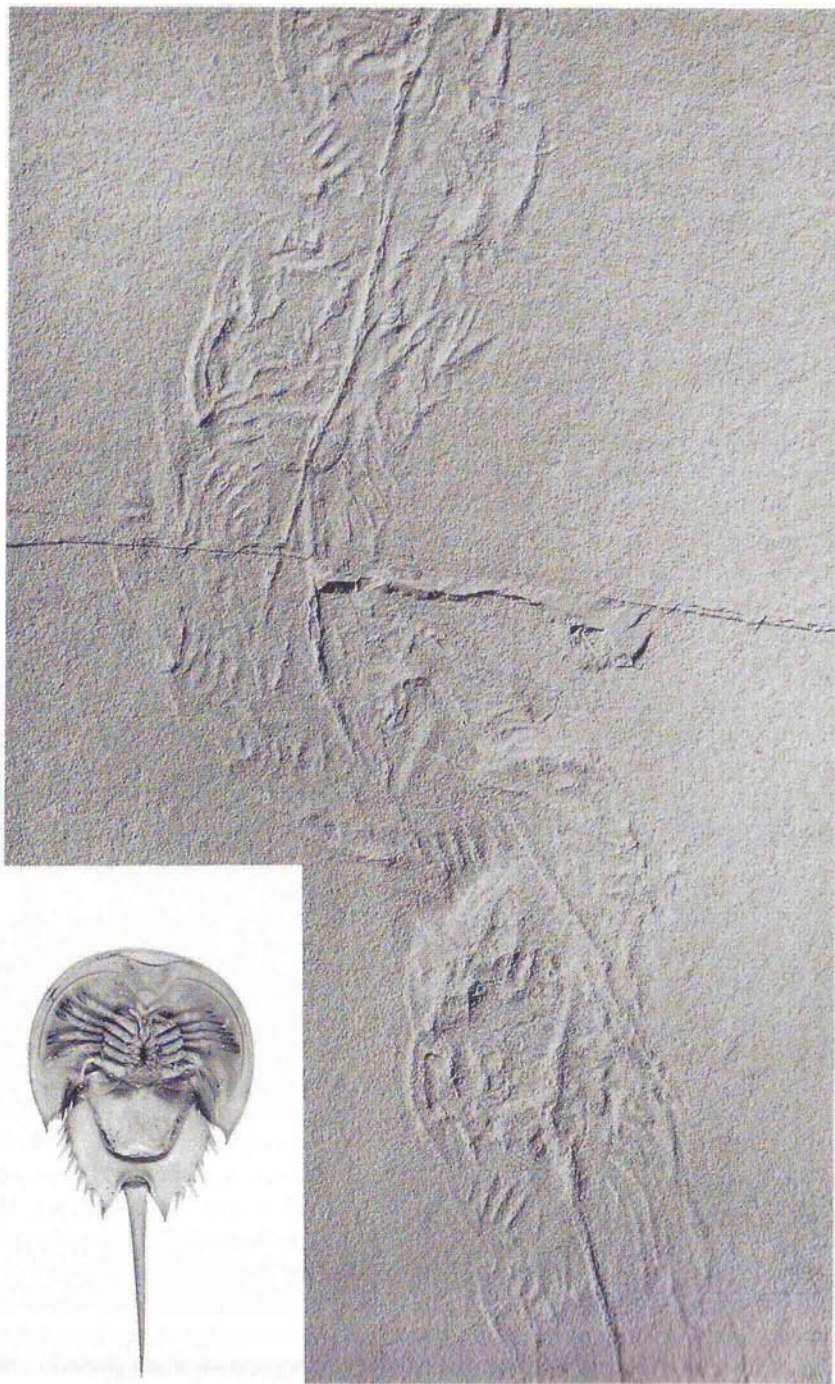
Fig. 5.8 Bivalved mollusc; *Solemya* sp., Eichstätt; cast of an original destroyed in the war from BSPHGM; bivalve 10 mm long; JME.

Fig. 5.6 (inset opposite)   Xiphosuran chelicerate; moult of modern *Limulus polyphemus* (Linné), Florida; length 141 mm; private collection.

Fig. 5.7 (opposite)   Xiphosuran chelicerate; *Mesolimulus walchi* Desmarest and walking track, Solnhofen; width of track at uppermost part of plate 105 mm; MSAV.

Fig. 5.9 Bivalved mollusc; *Solemya* sp., Eichstätt; cast of an original destroyed in the war from BSPHGM; bivalve 12 mm long; JME.

soft-bodied gorgonians (a group of cnidarians that are related to other corals) have been preserved, but there were almost certainly other soft-bodied coelenterates and many algae of which there are now no trace. The bulk of the reef frame was made of corals and encrusted by other corals, coral-like hydrozoans and calcareous algae, all adding to its strength. Inside cracks and crevices lodged brachiopods, attached by pedicles, as well as various bivalves that included clusters of mussels hanging by byssal threads to the substrate and oysters cemented onto the rock.

The calcium carbonate reefal structure broke up under the action of the waves into blocks of debris and finer sediment. Many organisms sought anchorage in the sediment. These included bivalves such as the triangular *Pinna*, and some holothurians, which by analogy with modern genera lived on or in the sediment (as well as contributing to it by the dispersal of the ossicles on death). Ophiuroids probably sat on the sediment and lived off organic matter suspended in the water. Microorganisms such as benthic foraminifera and ostracods lived on the sediment and, on death, contributed to its accumulation. There are also some examples of fully infaunal organisms. These included some bivalves, such as *Solemya* (which makes the trace fossil, see figs 5.8 & 5.9), and polychaete worms such as *Ctenoscolex*. Other benthic invertebrates, such as many crustaceans and the limulids, were capable of shallow burrowing in search of these organisms as prey, whilst others, such as the irregular echinoids, were deposit feeders. Of the vertebrates, sharks and rays slithered over the bottom and grubbed around in the sediment for shellfish. Another section of the vagile or mobile benthic community, particularly the gastropods, regular echinoids and starfish, was adapted to surface grazing. These organisms concentrated their activities on the reefal structure where they ate algae and

Fig. 5.10 Gastropod; *Rissoa* sp., quarry above Gungolding–Pflalzpaint; gastropods are around 5–8 mm long; JME.

sometimes munched coral polyps. In turn other echinoids, many crustaceans and smaller fish no doubt fed on the grazers.

There is a fine dividing line between those organisms to be considered as vagile benthos and those which settled so rarely on the bottom that they constitute part of the nekton. No doubt many of the smaller crustaceans, such as the shrimps, swam for a large proportion of their time, whilst of the fish some

Fig. 5.11   Gastropod; *Rissoa* sp., quarry above Gungolding–Pflalzpaint; 5.5 mm long; JME.

of the rays spent longer on the bottom. Of the more nektonic of the fish there were a great variety of life styles. The small, deep-bodied *Gyronchus*, analogous to modern parrot fish, must have been excellently adapted to weaving its way through the coral branches, nibbling at corals and darting away from predators. Shoals of the sprat-like *Leptolepides* probably swam vigorously around the reefs, occasionally gobbled up by one of the giant pachycormid fish or possibly by a turtle. Some fish, such as *Caturus*, with their torpedo-shaped bodies and forked tails, looked like the modern herring, suggesting that they too were inhabitants of more open waters. To this category we must add most cephalopods, certainly the squids, cuttlefish, nautiloids and perhaps (although this is more speculative) the ammonites and belemnites. The larger marine reptiles would probably have avoided shallow waters and so the ichthyosaurs, plesiosaurs and sea crocodiles most likely lived in the open sea. The weaker swimmers, or really floaters, lived in the quieter surface waters. Of these the jellyfish, and free-swimming hydrozoans and planktonic crinoids, were numerous and most susceptible to being swept into the lagoon.

Terrestrial ecosystems

The terrestrial environments to the north of the lagoon contributed plants, insects, reptiles and *Archaeopteryx* to the Solnhofen Plattenkalk. As they have been removed from the geological record by erosion, their reconstruction must

Fig. 5.12   Malacostracan crustacean; *Mecochirus longimanatus* (Schlotheim), Maxberg bei Solnhofen; length of animal 150 mm; MSAV.

be to some extent speculative. In all probability the land was low-lying and of no great areal extent because it did not supply any appreciable amount of terrigenous sediment to the lagoon. River channels were not a permanent feature of the landscape, but freshwater ponds probably existed seasonally. There may have been a belt of wide sandy beaches fringing the land.

In the hinterland, the stunted, shrubby growth consisted mostly of gymnosperms, able to survive in this dry, salty soil (see reconstruction, fig. 5.13). Seed ferns, particularly the widely dispersed and presumably hardy *Cycadopteris*, formed a scanty undergrowth whilst squat, cone-bearing cycadophytes, deciduous-leaved ginkgos and stunted, scaly conifer bushes were present as isolated shrubs. No logs have ever been recovered from the Solnhofen Plattenkalk and one conclusion may be that trees were either very rare or absent from the land immediately adjacent to the lagoon. However, further to the north lay the landmasses of the 'Mitteldeutsche Schwelle' and the London-Brabant Massif (fig. 2.7, p. 26) and they most probably held richer plant as well as animal communities. The plants produced various megaspores, cones and pollen, which would have supported a diverse insect population. Of the insects recovered from the Solnhofen Plattenkalk, most are dependent on a freshwater habitat for the larval stages of their life cycle.

Into this setting we can place the land reptiles and the renowned *Archaeopteryx*. The rhynchocephalians and small lizards most likely spent much of their lives basking in the sun and running under stones. They probably ate insects and were themselves eaten by the fast-running little dinosaur *Compsognathus* (a lizard has been found in the gut contents of the one known specimen of *Compsognathus*). The relatively common pterosaurs lived in close proximity to the lagoon and with their large wings and light bodies they must have been adept fliers. Some were probably water animals as they have webbing between their hind toes and many ate fish, judging from the stomach contents. However, one genus, *Ctenochasma*, has teeth, which suggest that it was more likely to have been an insectivore.

How *Archaeopteryx* lived really depends on the function we attribute to its feathers. The feathers of primitive birds could conceivably have served a number of purposes, such as body insulation for a warm-blooded beast (e.g. Bakker 1975), a heat shield (Regal 1975), an insect trap (Ostrom 1974) or for display (Cowen & Lipps 1982). But it is a different, and slightly less speculative question as to the function of the feathers on *Archaeopteryx* itself. The primary wing feathers, as seen on the Berlin specimen and on the lone feather, are obviously asymmetrical and, in modern birds, this excellent aerofoil shape is possessed only by those who are capable fliers (Feduccia & Tordoff 1979). In addition, the shape of the *Archaeopteryx* wing and the distribution of different types of feathers are essentially the same as in modern flying birds. So, granted that *Archaeopteryx* is likely to have flown, the debate continues as to whether it was capable of flapping flight, or merely gliding. It had been suggested that the
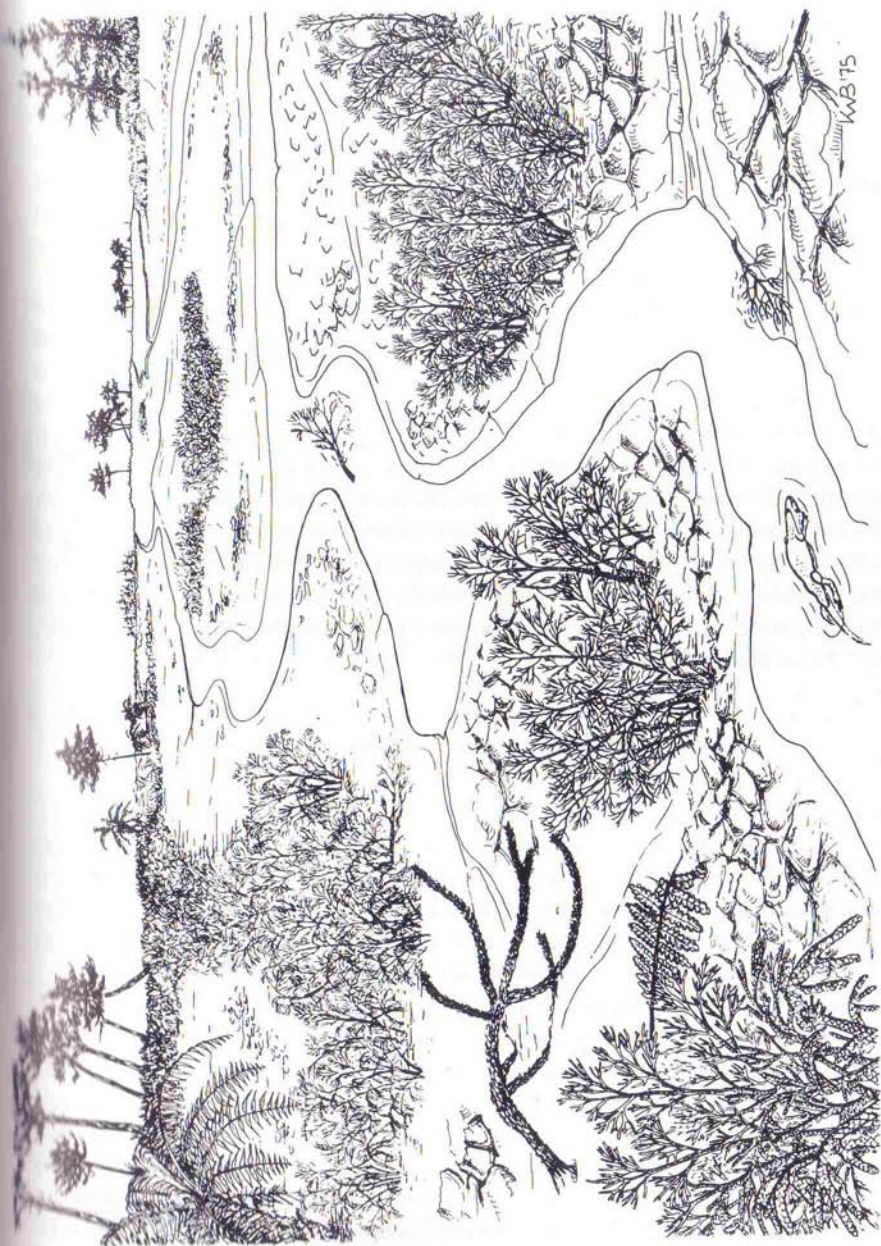
Fig. 5.13 Palaeoecological reconstruction of plant communities on land adjacent to the Solnhofen lagoon.

shoulder girdle could not have borne a musculature suitable for flapping flight (Walker 1972, Ostrom 1976), the essential points being the lack of the keel for the attachment of the muscles necessary for the strong flight downbeat (see also discussion of *Archaeopteryx*'s morphology, pp. 191–201) and the lack of a bony process for the operation of a pulley system to raise the wing. These objections to *Archaeopteryx*'s capability as a good flier were countered by Feduccia & Tordoff (1979) who pointed out that the pectoral muscles involved in the downbeat could attach elsewhere, in particular to the large furcula, and that the muscles used to raise the wing in more advanced birds were not essential (Sy 1936). There seems now no reason not to accept *Archaeopteryx* as a capable flier.

Archaeopteryx might have been either a ground or a tree-dwelling bird. On the ground it could have used its long legs for running, although it is doubtful whether it could have run fast enough to take off. Safer with regard to predators would be an arboreal life. As already mentioned, no trees are found fossilized in the Solnhofen Plattenkalk, but *Archaeopteryx* could have been buried at quite some distance from its normal habitat so that this in itself is not a strong objection to an arboreal habitat for the bird. In the trees, *Archaeopteryx* could have used its claws to climb up trunks. It walked along branches using its wings to balance and then launched itself into the air. In the trees it probably ate insects which it chewed with its small teeth. (For a further discussion of the subject the reader is referred to the volume of the *Archaeopteryx* conference, edited by Hecht *et al.* 1985.)

6 Taphonomy

Introduction

Despite the incredible fidelity of preservation and the richness of the major collections, the fossils from the Solnhofen Plattenkalk do not represent complete Jurassic ecosystems, frozen for our inspection. The animals and plants derived from the various terrestrial and marine habitats represent a selective sample, biased firstly during transport into the lagoonal basins, and secondly by differential decay and dissolution in the sediment. The study of all those processes affecting the potential fossils, from their transport into the lagoonal waters, death (although 'death march' traces have been dealt with in the chapter on palaeoecology) and ultimate exhumation of the fossil, falls into the domain of **taphonomy**. This major topic is subdivided into **biostratinomy**, where events from death to final burial are discussed, whilst **diagenesis** encompasses all those changes occurring within the sediment.

Biostratinomy of the marine biota

The marine organisms in the Solnhofen Plattenkalk lived in and around the coral reefs on the northern margin of the Tethys Ocean. As monsoonal winds whipped up storms over the sea, waves crashed against the reef and swept water over into the lagoon. Occasionally, living organisms were entrained in the flow and were carried over the reefs to be submerged in the lagoonal brines.

The organisms of the reefal ecosystems were, in effect, 'siphoned off'. Those most likely to be swept away were the organisms which floated in the surface waters, such as the planktonic crinoids and jellyfish. These were followed by the weak swimmers, the small fish and ammonites. In lesser abundance came the stronger swimmers, such as the squids and cuttlefish, and the non-anchored benthos, which included the limulids and many crustaceans. (These groups of organisms, in particular the crinoids, small fish and crustaceans, as well as ammonite shells, comprise the greatest number of fossil specimens collected.) The weakly attached reefal organisms, such as the brachiopods and the shallow infaunal sediment dwellers, of which many bivalves, other crustaceans and the polychaete worms are examples, would be less likely to be removed. It would

also have taken a strong storm to have carried one of the larger fish, a crocodile, or a plesiosaur into the lagoon. Lastly, the strongly attached reefal organisms, the framework builders, binders, encrusters and crevice dwellers are only represented by fragments in the plattenkalk sediment which travelled short distances. It is, after all, only the finest sediment stirred up from the seafloor which was washed into the inner lagoon. In this influx, most living organisms were either left behind or else they swam back out of danger.

In the central and western regions of the plattenkalk area, there are cases where tens or even hundreds of animals of the same species are found strewn over a single bedding plane. Evidently currents carried away local, perhaps seasonal, shoals through gaps in the reef. The best example of this are the juvenile crinoid *Saccocoma* (fig. 7.49) and the small fish classified as *Leptolepides* (fig. 6.4), which are both occasionally found in large numbers in the Eichstätt quarries. In addition there are numerous well-preserved jellyfish from the Gungolding–Pfalzpaint area. The abnormal regional abundance of ophiuroids from Zandt (see p. 64) may represent opportunistic colonization of the lagoon floor (but not at the site where the animals are now buried). Death in all these cases was effectively instantaneous as there are no tracks or signs of a death struggle on the lagoonal sediment. (The few animals which were still alive in the lagoon are discussed under palaeoecology, pp. 77–9).

Amongst the early post-mortem features to develop was the osmotic wrinkling of normally turgid animals when bathed in these hypersaline solutions, as exemplified by some jellyfish. In other animals there was an early contraction of tendrils, and muscles fibres. The arms of the crinoid *Saccocoma* (fig. 7.49, p. 154) have tips which are strongly coiled, whilst the bases are straight. In contrast, a slightly differently constructed crinoid, *Pterocoma* (fig. 7.51, p. 156), has arms with rigid tips, but bases extensively coiled (Seilacher *et al.* 1985). In some shrimps, such as *Penaeus*, muscle contraction after death has caused the tail to curl up, sometimes scraping off the surface of the sediment towards the body (Mayr 1967). Most striking is the backwards bend in the vertebral column of some fish (fig. 6.4, pp. 94–5). Sometimes this is so pronounced that the head became disarticulated from the body.

After death the bodies started to rot. The rate of decay was greatest when the bodies floated in the surface waters, slower when under the hypersaline brine (see special preservation, pp. 59–63), and slowest of all when the bodies were encased within sediments that rapidly became anoxic. So, whilst the exceptionally preserved fossils were delivered straight to the hypersaline pools to be covered rapidly by sediment, the less well-preserved specimens (which are relatively quite common) drifted around in the surface waters before becoming entombed in the sediment. Some corpses remained buoyant in the water column because gas generated by their decay remained trapped. The air-chambered cephalopods may have drifted for some time whilst the soft body decayed and detached itself from the skeleton (see fig. 6.1). Some belemnite
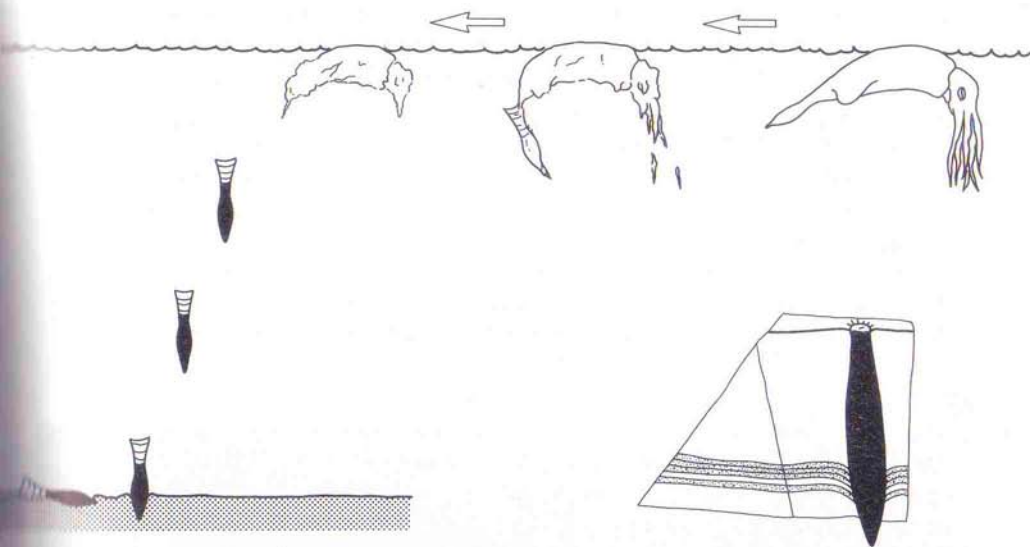
Fig. 6.1 Disintegration and burial of the belemnite animal. The belemnite hard parts may drop into the sediment and remain undisturbed by current activity.

skeletons which continued to drift after the soft body had fallen away were then encrusted by oyster larvae, the relative size of the oyster shells demonstrating for how long the belemnite had drifted. When the guard and phragmocone ultimately sank to the sea bottom, it hit the sediment with some force, distorting some of the underlying laminae. Gas trapped inside the abdominal cavity probably accounts for the poor preservation of some fish. The bent fish were suspended belly-up just above the sediment–water interface, leaving the tail free to brush over the sediment surface with the scales being scattered down current. Some fish from the Solnhofen–Langenaltheim area are even less well preserved. The bones of the head, pectoral fins and backbone with ribs and tail are still present, but the dorsal fin, scales and pelvic girdle with fins are missing. Finally the fish, *Aspidorhynchus* and *Belonostomus*, can show a peculiar kind of preservation (fig. 7.66, p. 175). As with other fish the post-mortem feature to develop is the head detaching from the rest of the body, though in this case instead of the scales being lost, the skeleton comes away from the skin leaving a 'scale envelope'.

In the plattenkalk basins the currents which acted on the corpses, shells and other fragments were generally weak, but locally variable. In some of the quietest places, such as the Eichstätt basin, as the bodies wafted down through the water column they first settled in a place slightly adjacent to where the body fossil is now found. The best example of a transitory resting impression is a specimen of the rhynchocephalian, *Kallimodon* (see fig. 7.78, p. 183). The tail

seems to have been anchored in the mud and the front of the body swung around (see also fig. 6.2 for a comparable example in a fish). In an assessment of current activity in the Eichstätt basin, made at the Jura-Museum site at Schernfeld (Viohl 1985), ammonite aptychi and fragments of ammonite shells were all found concave-up (fig. 6.3), a position that is unstable in a current. At other times currents may have been slightly stronger. On the rare occasion when many elongate fossils are found together, such as in the Solnhofen, '*Fischflinz*' (see fig. 6.4), the fossils are roughly parallel to each other and to the presumed current direction. Overall, however, such current activity was minimal to judge from the general lack of any current indicators. As mentioned on p. 68, the commonly cited palaeocurrent indicators of the plattenkalk come

Fig. 6.2 Circular dragmark around fish embedded in micritic mud, Mühlheim bei Mörnsheim; distance between the two points of the tail 66 mm; JME.
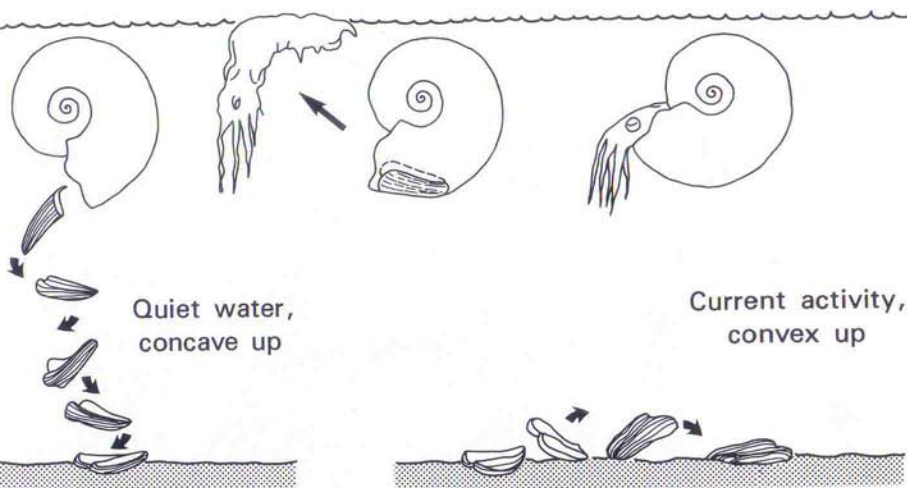
Fig. 6.3 Disintegration and burial of the ammonite animal. Note the orientation of the aptychi is controlled by current activity.

from the quarries at Kelheim and Painten, but these examples of scratch marks and ammonite rollmarks almost certainly occur at the base of turbidite beds, and represent local directions of the palaeoslope of the basin floor rather than a general palaeocurrent direction.

Biostratinomy of the terrestrial biota

Terrestrial fossils, such as the insects, ground-dwelling and flying reptiles and of course *Archaeopteryx*, are some of the best known of the exceptionally preserved fossils. As explained on p. 56, the preservation of the terrestrial fossils was initially interpreted as the desiccation of corpses stranded on the shoreline. If the muscles dried out, the argument went, the tendons would contract and produce the sharply bent back neck which can be clearly recognized both in *Archaeopteryx* and the pterosaurs. But this kind of feature seems to be normal for long-necked terrestrial animals (Ostrom 1978) and, as discussed above, the fish which were always submerged show a similar feature. If, as discussed by Viohl (1985), *Archaeopteryx* had first lain on the sea-shore, air would have been trapped in the lungs and feathers and this would prolong the drifting time to perhaps 30 or 40 days, by the end of which time the body would have largely decomposed. It is thought that the best preserved of the *Archaeopteryx* specimens could not have drifted for this long. Most probably, the airborne birds were caught in high winds and waves and were drowned. With the lungs full of water and the plumage soaked, the bodies sank to the

Fig. 6.4 Solnhofen '*Fischflinz*', *Leptolepides sprattiformis* Agassiz, probably from the Solnhofen area; natural size; BSPHGM AS I 819.

bottom (Schäfer 1962, 1976, Rietschel 1976). *Archaeopteryx* came to lie on its back, chest uppermost and wings outstretched on the lagoon floor. Even in the best specimens, feathers are only preserved on the wings and the tail (and possibly the back of the head). In modern bird carcasses we see the same initial stages of decay, first the loosely attached contour and down feathers are lost from the back and the breast, and the most strongly attached flight feathers remain the longest.

Of the Solnhofen Plattenkalk insects, only flying forms are recorded. This is perhaps hardly surprising, the offshore winds being most likely to entrain them and blow them across the lagoon. Most insects have come from Eichstätt and Kelheim quarries, which could be because the original insect habitat lay somewhere to the east or simply due to the prevailing wind conditions. The insects may have drifted on the surface of the water for a few days and then sank to the bottom, in most cases with wings outstretched.

Plant fragments could also have been blown into the lagoon, or else delivered by small freshwater streams. In any case plant material is never common in the Solnhofen Plattenkalk, and (as mentioned in palaeoecology, p. 86) large pieces such as logs do not occur. Plant material is more abundant in the beds which underlie the Solnhofen Plattenkalk at Painten, and in overlying beds at Daiting. The reason why only small fragments occur may be that trees did not grow on the adjacent land, or that water transport was never sufficiently strong to carry them into the lagoon.

Fossil diagenesis

Most corpses were delivered to the lagoon to be covered immediately by a rain of micritic sediment although a few which lay for a while on the lagoon floor may have been overgrown by cyanobacterial mats (see pp. 64–5). The micritic sediment rained down vertically upon the corpses, and current activity was rarely sufficient to push sediment into all the nooks and crannies. Water-filled cavities were sometimes left beneath some shells, later to be infilled by sparry calcite. Ammonite shells generally still contained the soft body (Seilacher *et al.* 1976) and so were not infilled by sediment apart from a plug at the aperture (presumably because the body had been pushed back inside the body chamber). The soft ooze consolidated around the bodies. Buried beneath a growing pile of sediment the corpses were physically compacted and chemically altered.

Whilst most of the fossils are found at the interface between two beds with the actual body adhering to the upper bedding plane, some (in particular the insects and limulids) are a few millimetres above this interface and just inside the overlying slab. Thus the sediment which covers the fossil must be chiselled away. Fossils which had a certain amount of relief at the time of burial, but

which have since been squashed flat, have a peculiar type of preservation. Fig. 6.5 records the sequence of events in the fossilization of an ammonite shell, which has left impressions on both the upper and lower bedding planes. On the top of the lower slab the fossil stands slightly elevated from its surroundings, as if on a pedestal, and it fits into a hole in the bottom of the upper slab (a feature known in German as '*Sockel-Erhaltung*'). On the top of the upper slab there is a depression corresponding to the collapsed body underneath so that if a fossil were present on one of the minor partings inside a flinz slab it would not escape attention. Fig. 6.6 shows both part and counterpart of an ammonite which nicely demonstrates this preservational feature. Pedestal structures are a characteristic although not exclusive phenomenon of the Solnhofen Platten-kalk. They are also known in other deposits where soft-part preservation occurs, representing environments where decay was very slow and the bodies resisted initial sediment compaction.

The animal bodies lay on the lagoon floor (fig. 6.5a) and as each pulse of sediment settled over them, a new lamina draped the bodies. This deflection of bedding over the site of the fossils became less marked with subsequent laminae and was eventually evened out (fig. 6.5b). As sediment continued to
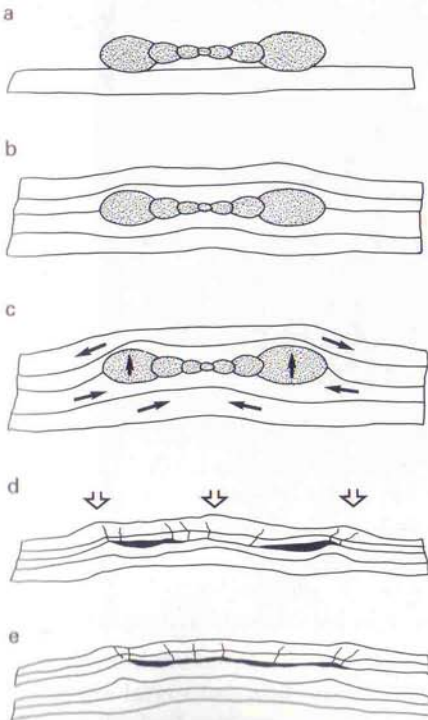
Fig. 6.5 Burial and diagenesis of an ammonite shell to form a pedestal and socket. (a) Ammonite shell lies on the sediment surface with its chambers full of water. (b) Entombed in sediment. (c) Under pressure of burial the buoyant ammonite shell, without sediment inside, is pushed upwards deflecting sediment laminae. (d) Under increased pressure the shell caves in. (e) As the rock splits along the bedding plane the ammonite lies in a depression in the overlying slab and on a pedestal on the underlying slab.
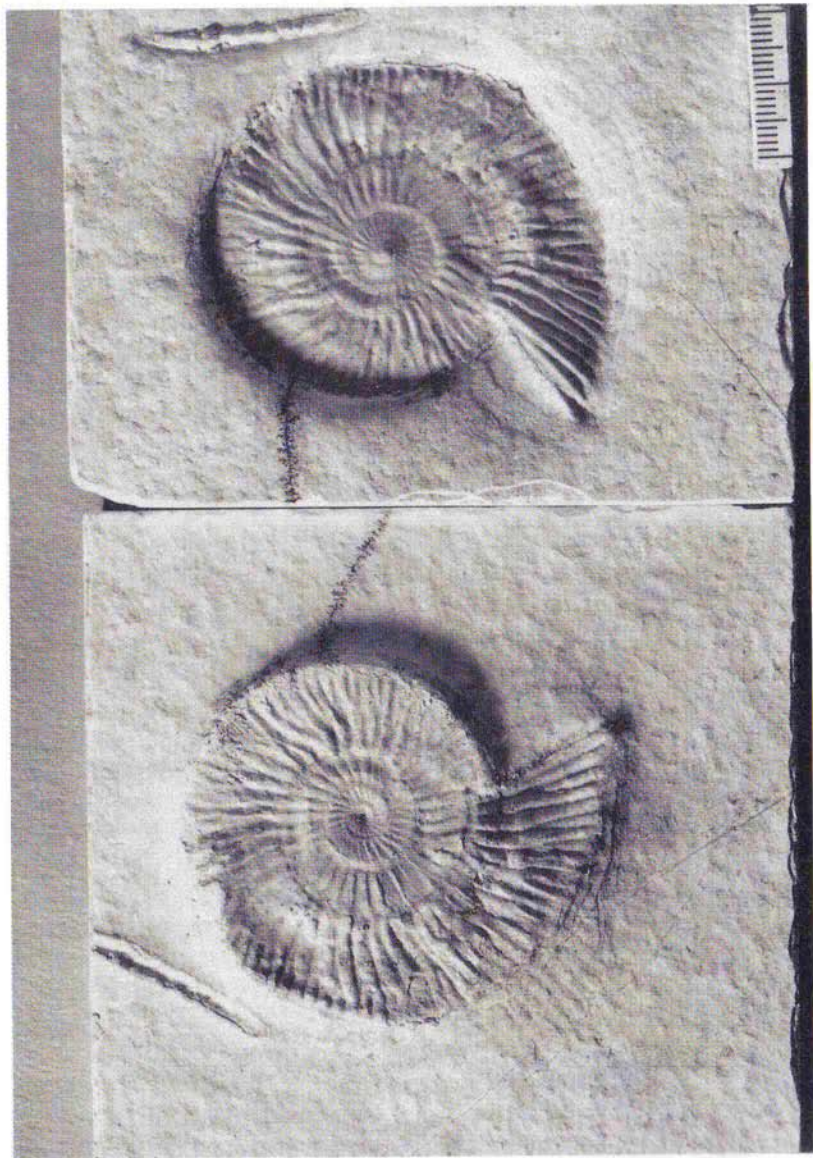
Fig. 6.6 Ammonite *Subplanites* sp. showing typical pedestal and socket preservation ('Sockel-Erhaltung'). On the left is, what would have been, the underlying slab with the ammonite on a pedestal. On the right, in the overlying slab, the ammonite lies in a depression. Courtesy of the Jura-Museum, Eichstätt, photo W. Balling.

accumulate on top, water was squeezed out of the underlying beds. At this stage the fossil must have risen slightly within the sediment, as a result of differential compaction between the resistant fossil and sediment. This elevation of fossils can be demonstrated in the occasional uncollapsed specimen such as the ammonite figured by Janicke ((1969, pl. 7, fig. 1), cited in Seilacher *et al.* 1976) where both the under and overlying laminae are bent upwards. The soft tissue was weakened by decay while the aragonite of the ammonite shells progressively dissolved. As the pressure increased, the previously resistant bodies gave way and collapsed, so that laminae both above and below are deflected towards the fossil (fig. 6.5d).

The plattenkalk fossils show features which demonstrate the relative timing of sediment cementation and fossil diagenesis (Seilacher *et al.* 1976). Some fossils, notably shrimps, small fish and squids, collapsed before the sediment was lithified and produce a corresponding smooth crater on the upper surface of the bed. Other fossils must have been more resistant and collapsed at a later stage, after the sediment was lithified. Hence the ammonite *Perisphinctes* produces a steep-walled, faulted 'caldera' rather than a smooth depression in the top surface of the slab. Other ammonites, such as *Oppelia*, clearly collapsed in two distinct steps. The relatively frail wall of the body chamber caved in before the stronger phragmocone. Between these two events, the phragmocone supported cavities which became infilled by calcite. These patches of calcite end abruptly in a distinct line along the final septum which partitions off the body chamber.

Whilst most of the fossil bodies have collapsed to effectively two-dimensions, sometimes the original three-dimensional structure has been preserved by the precipitation of calcite inside the fossil. Growth of calcite may have happened at various stages of diagenesis. A case of very early cavity infilling was the precipitation of calcite in the abdominal cavities of some fish, where decay gases were most probably trapped, and the eye sockets of the squids. Crystalline calcite is found in the inner chambers and along the keel of ammonite shells which were presumably strong enough to resist initial compaction. Whilst sometimes calcite preserves details which otherwise would have been lost, generally it is detrimental to the fossil preservation as the hard crystalline calcite distorts the shape of the fossils during later compaction and can make the fossil difficult to prepare for museum display.

Another way in which some of the three-dimensional structure of the body may be preserved is by early cementation of the surrounding sediment, so producing a concretion. A similar process may be seen on beaches today around stranded whale carcases, where soft fat leaking into the sediment produces a strongly alkaline environment that induces precipitation of calcium in and around the corpse. In plattenkalk fossils, concretions are most common around the larger fish and reptiles and are readily recognizable as they bulge out from the bed surface.

Chemistry of fossil preservation

Once buried in the sediment, the pore waters rapidly became sealed from the overlying waters and strongly reducing conditions set in. Due to the very slow activity of the microbial decomposers, decay of soft tissue was so retarded that the shape of the fossil body was imprinted on a surrounding mud, which already possessed a degree of cohesion. Much fine detail of the soft tissue is therefore preserved as impressions, e.g. the wing veins of insects and pterosaurs or the feathers of *Archaeopteryx*. Indeed, the detailed study of the Berlin *Archaeopteryx* by Rietschel (1985) has revealed some very interesting and unexpected details. The underside of the wing and hence of the feathers is preserved on *both* slabs. On the main slab, which contains most of the bones and which was the overlying slab, the feathers are preserved as impressions and on the counter- (underlying) slab they are casts. Thus the feather material decayed away leaving a cavity which was infilled by sediment which 'oozed' from the side so taking a very early impression of the feather. On some fossils the impressions are enhanced by a residue of original organic matter. For example, the isolated feather of *Archaeopteryx* is quite black in places. Another example of organic preservation is the dry black powder found inside the ink sacs of some squids, which if redissolved in water will produce a usable ink. Cellulose is rarely preserved in the alkaline conditions of organic-poor lime sediments, so plant material is preserved only as impressions, sometimes lined by a thin carbon film. In some insects the impressions of the wings are very clear because of the precipitation of iron oxide in the veins (e.g. *Libellulium*, fig. 7.38, p. 144). More extensive mineralization has preserved structures that would otherwise have been lost. In particular, certain parts of fossils have been replaced by the phosphate mineral francolite. Most notable are the criss-cross muscle fibres of some fish, squids and insects.

The preservation of the soft tissue is, of course, the exception and the more usually preserved 'hard parts' account for the majority of the fossils. Some appear to have undergone relatively little alteration and are close to their original composition: bones, teeth and fish scales are still made of calcium phosphate. Chitin, the resistant proteinaceous material, still apparently forms the exoskeleton of arthropods, especially when reinforced by original calcite. Structures which were originally made of low-Mg calcite, such as the ammonite aptychi and belemnite guards, are preserved best of all. However, those shells or parts of shells made of aragonite dissolved, and ammonites, for example, are preserved primarily as impressions. Sometimes the impression is lined with the original outer organic membrane, the periostracum, and sometimes calcite has begun to infill the slight void left after the shell dissolution, usually forming little more than a calcitic film. Gastropods and some aragonitic bivalves are also preserved as impressions and sediment infilled moulds. The aragonitic dissolution of these shells must have occurred at quite shallow depths as the

ammonites in the Krumme Lage slump beds (see p. 37) occur as thin, contorted films. Another relatively unstable form of calcium carbonate, high-Mg calcite, of which echinoderm plates are made, has recrystallized during diagenesis but the plates have generally not lost their internal structure.

7 The fossils

Introduction

In this chapter the fossils themselves are described. They are arranged taxonomically, in an order which tries to reflect the closeness of their evolutionary relationships. We describe the basic construction of the fossil organisms and, by analogy to their nearest living relatives, show the ways in which they probably functioned. To get an idea of some of the variety of creatures which were alive in the Late Jurassic, it is not vital to stick to a system of rigidly defined taxonomic levels. Indeed, these have been studiously avoided because we feel that the more advanced reader would certainly find any attempt at rigorous classification already out of date and the less advanced would soon become bogged down in a superfluity of latinized names. But in general the major headings divide the fossils into phyla, whilst minor headings separate into subphyla and, in very diverse groups, orders. Usually only one genus is described in any detail, although sometimes others are mentioned to show the variation at the level of genus. A list of recorded Solnhofen genera is given in the appendix but it should be borne in mind that this is in need of major revision and that many of the Solnhofen fossils have not received detailed appraisal since the last century.

MONERANS AND PROTISTS

The **monerans** are prokaryotes, the simplest of unicellular organisms without any internal organelles and differing in major respects from the remaining four kingdoms of eukaryotes. The moneran kingdom includes most bacteria as well as the cyanobacteria (blue–green algae), and these are thought to be represented in the Solnhofen Plattenkalk by small spherical bodies, around 10 μm in diameter, observed under the scanning electron microscope, interpreted as the calcified, cellular moulds of cyanobacteria. These have already been discussed in detail under sedimentology, pp. 45–7. In contrast with the monerans, **protists** have more complicated cells with membrane-bound organelles, such as a nucleus, mitochondria and, in the case of photosynthesizers,

chloroplasts. Protists were important sediment contributors to the plattenkalk sediment and they include the Foraminifera and Coccolithophorida, which have been discussed already in chapter 3 (pp. 44–6) with the petrography of the Solnhofen Plattenkalk. The second kingdom, the **fungi**, are as yet unknown in the Solnhofen Plattenkalk.

PLANTS

The record of fossil plants from the Solnhofen Plattenkalk suggests that the plant communities were not very diverse, but both land and marine plants are represented. Unfortunately the plants are usually poorly preserved, most of them present as impressions, but some retain original carbon structure.

Non-vascular plants

Brown algae 'phaeophytes'

These algae are relatively simple multicellular, macroscopic plants. They lived anchored to the seafloor in coastal and shallow-water environments. Although they were perhaps common along the Solnhofen coast, their fossils are poorly preserved and, given their unprepossessing appearance, are not numerous in the public collections.

Many specimens bear the name of ***Phyllothallus*** and consist of tangled masses of strap-shaped fronds resembling modern seaweeds, particularly brown algae. The fronds have a coarse, pimply surface, revealed by the microscope to be clumps of foraminifera and bryozoa which must have encrusted the living alga. The specimen shown in fig. 7.1 is attached to a piece of reef rock similar to the reefal limestone which occurs to the south of Solnhofen in the region of Neuburg an der Donau.

Vascular plants

Plants adapted for life on land protect themselves from desiccation by a protective layer of epidermal cells and tough cuticle. Water must be absorbed through the roots and it is transported through the vascular system, up the stem, to the leaves where photosynthesis takes place. The vascular system is strengthened by the development of lignified (woody) tissue.

Two major branches of vascular plants can be recognized: the **pteridophytes**, which include the ferns, horsetails, clubmosses, and the **spermatophytes**, or **seed-plants**, which include the **gymnosperms** (conifers and cycads) as well as

Fig. 7.1 Brown alga; *Phyllothallus latifrons* Rothpletz, Langenaltheim, distance from top of seaweed to underside of attached rock 266 mm; JME.

the angiosperms or flowering plants (which did not evolve until the Cretaceous Period). The pteridophytes reproduce by means of spores borne on the sporophyte plant, which is the dominant stage in the life cycle, although they also have a small and insignificant gametophyte stage, where sexual reproduction takes place. In the seed-plants the sporophyll stage is completely dominant, and the gametophyte stage no longer independent, but reduced to cells forming pollen grains and ovules (fig. 7.2). During reproduction, pollen grains are produced and then dispersed by the wind or by insects. The pollen fertilizes the ovules which remain on the plant and ripen to form seeds. These contain food reserves for the germinating seedling.

All the vascular plants so far determined from the Solnhofen Plattenkalk appear to be gymnosperms. Conditions were perhaps unsuitable for the pteridophytes, particularly the ferns, which are so common in other Jurassic deposits. The reason for this may be that ferns need damp habitats for the fragile gametophyte stage of the life cycle (where the sperm must swim through a film of groundwater in order to reach the egg) and they may have found the adjacent land too arid (see palaeoecology, pp. 71–3).
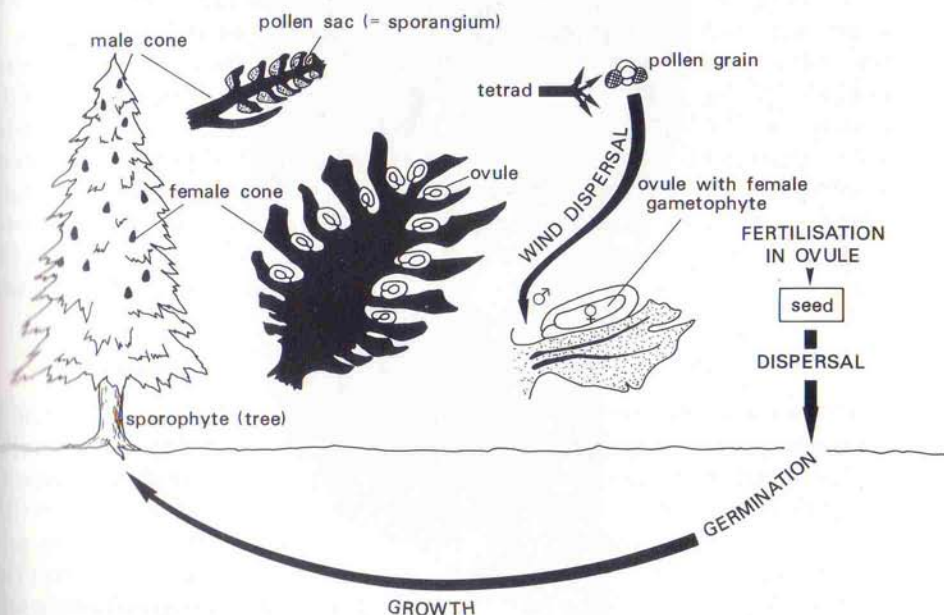
Fig. 7.2 Reproductive life cycle of gymnosperms. The tree produces male and female cones. Male cones give rise to pollen grains which are blown on to female cones of the same or a different tree. Fertilization of the ovule produces a seed on the tree which later falls to the ground and germinates. From Brasier (1980), reproduced by kind permission of Unwin Hyman Ltd.

GYMNOSPERMS

Seed ferns (pteridosperms)

The extinct seed ferns are the simplest and most primitive of all the gymnosperms. At first sight the leaves look identical to fern fronds, but rather than spore capsules on the underside of the leaf, there are pollen sacs or true seeds.

Cycadopteris (fig. 7.3) is a common and widespread Jurassic genus. Its fern-like fronds reached lengths of more than a metre, but it is the smaller sub-units of the fronds, the pinnae, that are more common as plattenkalk fossils. Set on either side of a strong central axis, the pinnae vary in shape. At the base of the

Fig. 7.3 Gymnosperm; *Cycadopteris jurensis* (Kurr) Schenk, Kelheim; length 142 mm; BSPHGM AS I 816b.

frond they are round or tongue-shaped, towards the apex they become large and further subdivided, whilst at the tip they are again tongue-shaped. Both the pinnae and their subdivisions have a midrib and simple, rarely forking, fine leaf-veins. Specimens which are very well preserved may show that the leathery cuticle on the upper leaf surface is folded over at the leaf edges and the stomata are confined to the underside of the leaves. These features suggest that the plant was adapted to a dry climate (see palaeoecology, p. 72). Despite the many specimens of *Cycadopteris*, sporangia have never been found associated with the pinnae, as would be expected if the plant was a fern. Although the seeds are also unknown, the plant is ascribed to the seed ferns because its thickened epidermis is not a character typical of true ferns.

Bennettitales

The Bennettitales are related to the extant cycads. Modern cycads are tropical or subtropical trees with stout trunks, often short and stumpy, and ending in a crown of leaves. The leaves are tough, leathery and subdivided, or pinnate, and resemble palm or fern leaves. The Bennettitales have flower-like, bisexual cones and in this they differ from the cycads (whose cones are single-sex).

Zamites (fig. 7.4) is a name which refers only to the leaf fossils. From a central axis diverge alternating lance-shaped pinnae, all with parallel venation and superficially resembling a palm leaf (see also palaeoecology, p. 72). Without associated reproductive structures it is hard to tell cycad from bennettitalean leaves, but well-preserved material may show important differences in the stomata. *Sphenozamites* (fig. 7.5) is also probably a bennettitalean. The pinnae are more triangular in shape and joined to the stem at the apex of the triangle. The venation is fan-shaped. This is the only recorded example of this taxon from the Bavarian plattenkalks.

Ginkgos

The living ginkgo (or maidenhair tree, *Ginkgo biloba*), which is a native of China, is the only surviving member of this group. In many ways ginkgos are intermediate between the Cycadopsida and Coniferopsida. Fan-shaped leaves, either entire or bilobate with dichotomously branching venation, characterize the ginkgos. In the illustrated specimen (fig. 7.6), the venation is not well preserved, so that the two-lobed shape is really the only reason for placing it in the genus *Ginkgo* (and, incidently, there are modern algae which also have this shape). Unfortunately, the best ginkgo material from the Solnhofen Platten-kalk was lost during the Second World War. *Baiera* (not illustrated) is an important ginkgo genus with deeply divided leaves. Each leaf consists of a fan of long, linear segments, each about 10 cm long and 5 mm wide, which are united at the base. The leaves are borne in clusters on a short shoot which
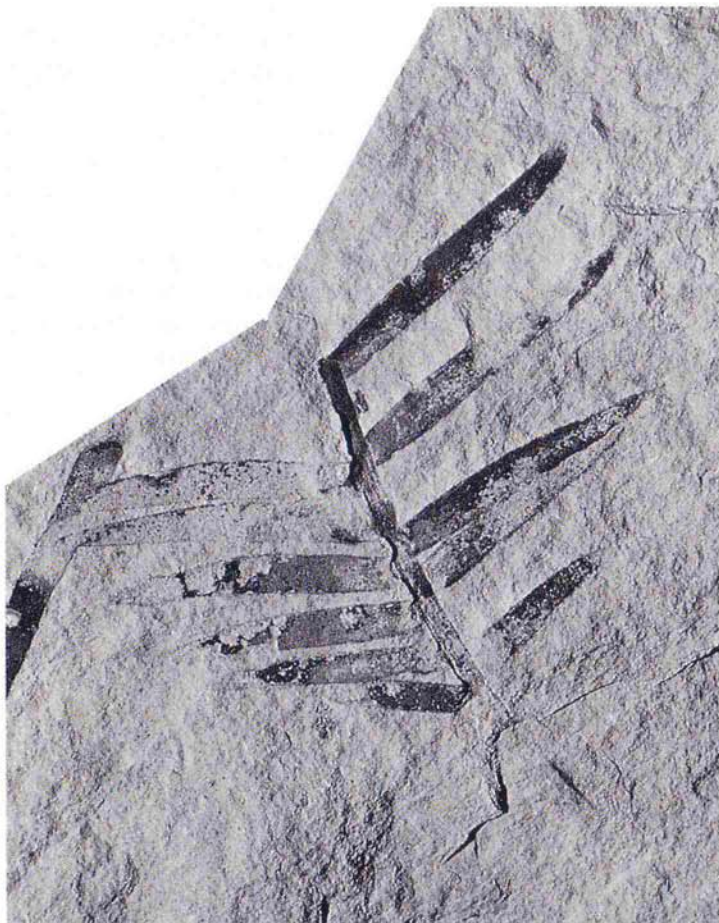
Fig. 7.4 Gymnosperm; *Zamites feneonsis* Brongniart, Bad Abbach bei Kelheim; stalk length 91 mm; BSPHGM 1972 VI 12.

terminates in a thorn-like tip and these shoots are carried on strong, mature branches.

Conifers (coniferopsids)

Today's conifers are typified by the tall trees of boreal and temperate climes with their needle or scale-like leaves. They generally have both male and

Fig. 7.5 Gymnosperm; *Sphenozamites latifolius* (Brongniart) Saporta, Eichstätt; length 192 mm; BSPHGM AS I 815 a.

Fig. 7.6   Gymnosperm; *?Ginkgo flabellatus* (Unger), Solnhofen; leaf length 36 mm; BSPHGM AS V 39.

female cones. The woody female cones surround and protect the ovules which occur in pairs at the base of the cone scales and in due course give rise to seeds. The male cones are much smaller and expose the pollen sacs.

Brachyphyllum is the commonest of the plattenkalk conifers and its leaf anatomy suggests it is related to the present-day monkey-puzzle tree (Araucariaceae family). A dense covering of small scale-like leaves is arranged in a spiral around the twigs and branches (fig. 7.7a). Cross-sections of the branches show an unusual feature; unlike other gymnosperms, which have well-developed wood, only the central part is lignified. This is a feature of many modern halophyte (i.e. salt-resistant) plants, so it is assumed that *Brachyphyllum* lived on salty soils and was a weak-stemmed, shrubby plant (see also palaeoecology, p. 72).

Palaeocyparis is figured in 7.8 (see also fig. 7.7b). It differs from *Brachyphyl-*
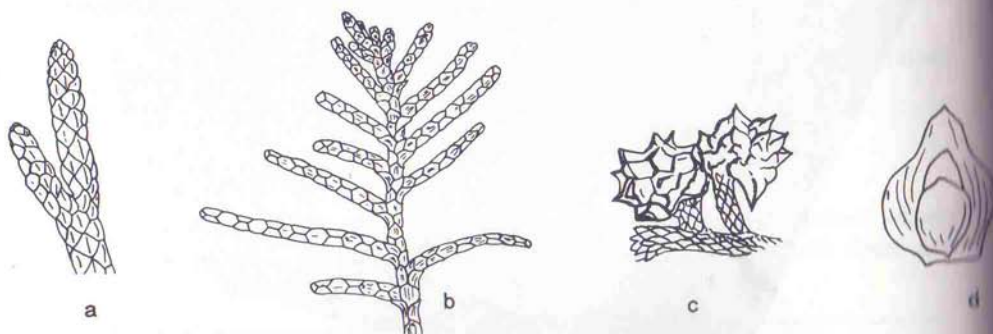
Fig. 7.7   Gymnosperms of the Solnhofen Plattenkalk. (a) *Brachyphyllum* twig; (b) *Palaeocyparis* twig; (c) *Arthrotaxites* cone; (d) Araucarian cone scale.

Fig. 7.8   Gymnosperm; *Palaeocyparis princeps* Saporta, Mörnsheim beds at Daiting; length 490 mm; BSPHGM 1964 XXII 149.

lum in the arrangement of its leaves on the smaller branches and twigs. The scale-like leaves are arranged in the shape of a letter X, with a central scale surrounded by four others, although on the larger branches the leaves are arranged in a spiral, as in *Brachyphyllum*. Both *Brachyphyllum* and *Palaeocyparis* are relatively common at quarries at Daiting in the west and Kelheim in the east. Cones are known only from one genus in the Solnhofen Plattenkalk, *Arthrotaxites* (fig. 7.7c), although isolated cone scales assigned to *Araucaria* (fig. 7.7d) have also been found.

111

ANIMALS

Invertebrates

SPONGES

Sponges are amongst the simplest of the metazoans with a bag-like body, variously folded in on itself and permeated by numerous canals. The body is supported by small needle-like struts, called spicules, made either of silica or calcium carbonate, which on occasion may grow into one another to make an interconnected structure. The form of the spicule is very useful in classifying the sponges.

Sponge thickets helped trap sediment and build the mounds which both underlie and subdivide the plattenkalk basins (see pp. 26–33). At the time of deposition of the Solnhofen Plattenkalk most of the lagoonal sponges were dead and so they are rarely found as fossils in the plattenkalk sediment. *Tremadictyon*, a sponge with an intergrown network of siliceous spicules (fig. 7.9), is found in the reefal localities of the Kelheim area. It almost certainly grew locally on the reefs, and avalanched into the basin when the sediment pile gave way. The sponge *Ammonella* is well known both from its body fossils, and from its spicules, which have three mutually perpendicular axes.

CNIDARIANS

Cnidarians are perhaps best known from the soft-bodied creatures such as the sea-anemone or jellyfish which demonstrate the radial symmetry. The body has a simple design of either a tubular polyp, or disc-like medusoid. One end has an opening surrounded by a ring of tentacles. This aperture serves as both mouth and anus and opens into a gut. During the life cycle there is often an alternation of body form. In the polyp stage the closed end of the elongate body is attached to the substrate and the tentacles dangle freely in the water. In the free-swimming, medusoid stage, the body takes on a much flatter, umbrella-like shape. The medusoid stage is the sexual stage of the life cycle.

Jellyfish (scyphozoans)

Scyphozoans are best known in their medusoid stage, and only fossil medusa have been preserved in the Solnhofen Plattenkalk. In the Scyphozoa, the mouth is on the underside of the bell-shaped body, is cross-shaped and

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Fig. 7.9 Sponge; *Tremadictyon sp.*, Kapfelberg bei Kelheim; maximum diameter 144 mm; BSPHGM 1975 I 109.

surrounded by small protuberances. Internal partitions divide the body into four lobes and there are four or eight gonads present. Both radial and ring canals occur. The edge of the bell has tentacles, either four or else a multiple of four in number.

The Solnhofen Plattenkalk is renowned for its jellyfish, most of which have come from the quarry region of Gungolding–Pfalzpaint where their presence in four different horizons is recorded. Isolated occurrences are also known from the Eichstätt area where they are not as well preserved. The impression of the lower surface of *Rhizostomites* (fig. 7.10) is illustrated. Often over 50 cm in diameter, this is one of the largest, as well as the commonest of the plattenkalk

Fig. 7.10   Jellyfish; *Rhizostomites admirandus* Haeckel; quarry above Gungolding-Pfalzpaint; maximum diameter 320 mm; BSPHGM 1875 XIV 55.

jellyfish. It shows two zones of circular muscle separated by a ring canal. In the middle of the animal is a cross-shaped mouth, surrounded by four gonads, whilst on the outside of the bell bunches of short tentacles may just be discerned. Groups of peripheral lobes, separated from each other by deep incisions, also typify the genus. An example of another plattenkalk jellyfish comes in the relatively rare *Leptobrachites* (unillustrated), smaller than *Rhizostomites* with a diameter of around 20 cm. It also has peripheral lobes but it differs in the possession of long, narrow oral processes and an absence of tentacles. Poorly preserved specimens of *Leptobrachites* are obtained from the Eichstätt area.

In the past, separate names have been given to the same species of jellyfish which are preserved in different ways. The figured example of *Rhizostomites* is an impression of the lower surface of the bell; in common with many such specimens it shows a concentration of ring muscles. Sometimes only the middle portion of the bell has left an impression. For example, specimens of *Rhizostomites* displaying bundles of tensed zig-zag muscles have been referred to as 'Myogramma'.

Jellyfish are not commonly fossilized and their preservation in the Solnhofen Plattenkalk is partly attributed to the hypersalinity of the water (see pp. 59–60) which also accounts for the wrinkling of some jellyfish specimens (presumably osmotic). The preservation of some of the jellyfish is unusual because they contain sediment inside the bell as shown in sections through jellyfish embedded in the rock. This sediment must have been pumped in by the jellyfish themselves presumably during their death throes.

Hydrozoans

Amongst the hydrozoans, the medusoid stage of the life cycle looks very similar to that of the scyphozoan jellyfish, but differs mainly in the possession of a flange on the underside of the umbrella (the velum) that is involved with locomotion. In the rare *Hydrocraspedota* (unfigured) the small flange has fine radial striations. The gastric cavity is undivided and the bell margin is not entire, but lobate. The mouth is square-shaped and surrounded by four kidney-shaped oral processes beyond which are four gonads. Tentacles are not well known, because they are generally very badly preserved.

Corals (anthozoans)

In the corals only the polyp stage is present with the medusoid absent from the life cycle. Corals may live singly, as in the soft-bodied sea-anemone, or as colonial organisms. Calcareous colonial corals were important framework builders of the southern coral reefs, such as those now exposed at Neuburg an der Donau. The polyps settled on a firm substrate, constructing a star-shaped

basal plate, with internal divisions numbering usually six (or a multiple thereof) and enclosed by an outer wall. As new polyps arise by budding the coral colony increases in size, its shape being determined by the species that built it. Fine fragments of these corals were probably important contributors to the plattenkalk sediment, although little unequivocal evidence of this remains.

There are also some examples of the preservation of soft-bodied corals in the Solnhofen Plattenkalk. The species in fig. 7.11 is tentatively attributed to the **gorgonians**, a group of corals with an eight-rayed symmetry. Gorgonians have a central axis made of proteinaceous material (keratin), which is only very rarely

Fig. 7.11 Part of a possible gorgonian; Solnhofen; MSAV.

fossilized, or else calcium carbonate. From this axis arise the polyp-bearing branches (see fig. 7.12, drawing of a modern gorgonian). The branches are made of small spicules of calcite which normally disintegrate on fossilization. The figured specimen resembles the living sea-fan *Iridogorgonia* in its construction and constitution, but is considerably larger.

ANNELID WORMS

Annelid worms are typified by the soft, squashable terrestrial earthworm. The essential characteristics of the group are the segmentation of the body and the bilateral symmetry. Worms are not exclusively terrestrial; there are also marine worms, some of which build themselves a tube-shaped casing of calcium carbonate, and these are quite commonly fossilized. These worms, mostly given the generic name of *Serpula*, were common encrusters in reefal environments in the Jurassic Period (as indeed they are today). Solnhofen serpulids lived on small pieces of driftwood and ammonite shells which floated into the lagoon.

There are also rare examples of free-living, soft-bodied marine worms, which lived either on or in the plattenkalk sediment. Two genera are recognized and the smaller of the two, *Ctenoscolex*, is illustrated (fig. 7.13). An impression of the segmented body can be seen together with the bunches of bristles, or chaetae. It is these structures that give their name to this group of annelid worms, the polychaetes. Chaetae are more prominent on the other worm, *Eunicites*, and there are also remnants of the jaw apparatus.

About 15 different genera and species of so-called Solnhofen 'worms' have been named, but most of them are too poorly preserved to provide certain identifications and, in fact, many may be fossil faeces (e.g. *Lumbricaria*, see figs. 5.1 & 5.2 under palaeoecology, pp. 75–6).

BRYOZOANS

The soft parts of modern bryozoans show that these animals are closely related to the brachiopods, as both show the same basic construction of a ring of
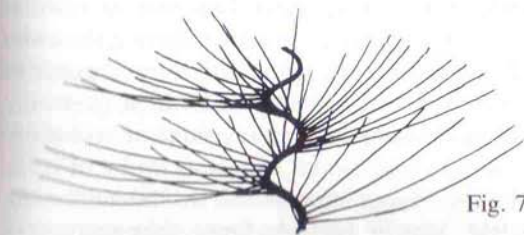
Fig. 7.12 Shape of a modern gorgonian.

Fig. 7.13 Annelid worm; *Ctenoscolex procerus* Ehlers, Zandt; measurable length 71 mm; BSPHGM AS V 26a.

ciliated tentacles surrounding a mouth, known as the lophophore. However, in the fossilized remains of these two groups of organisms no such similarity is apparent because all that remains of the bryozoans are the calcium carbonate casings which housed the colony. The often stick-like tubes are permeated by millimetre-sized pores which represent the openings of the chambers which housed the original individuals.

Common in reefal environments, in the Solnhofen Plattenkalk bryozoan fragments are frequently observed in thin-sections of coarser carbonate debris from near the coral reefs and as encrusters on objects which floated into the lagoon.

BRACHIOPODS

In living brachiopods, the lophophore, homologous to the feeding structure of the Bryozoa, is also used for respiration and food gathering. Frequently supported internally by a calcified loop, the lophophore often consists of two spirals, one each side of the median plane of the valves. The symmetry of the soft parts is mirrored in the shape of the shell. Each brachiopod valve is bilaterally symmetrical, whilst the two valves are of slightly different sizes and shapes. The larger of the two valves sometimes has a hole for the emergence of the pedicle, a stalk used for attachment. In some lineages of brachiopods, the pedicle may atrophy during growth or has been lost in the course of evolutionary history.

Today brachiopods are uncommon, being supplanted by the molluscan bivalves in most areas of the world. But in Jurassic times they were very

common and they came in two main forms, the smooth-shelled **terebratulids** and ribbed **rhynchonellids**. Both inhabited reefal environments where they lived inside nooks and crannies, attached to the reef rock. Although reasonably common and growing up to some 10 cm in size in the Kelheim area, in the Solnhofen Plattenkalk they are rare and when found are, without exception, compressed.

The terebratulid genus *Loboidothyris* accounts for the largest number of brachiopod species. Of the rhynchonellids *Septaliphoria* and *Lacunosella* deserve mention. Both have a small beak where the pedicle exited the shell. Whilst *Lacunosella* is symmetrical and coarsely ribbed, *Septaliphoria* is slightly asymmetrical with respect to the midline of the two valves. Another species of *Lacunosella* has three lobes, the middle lobe being especially broad.

MOLLUSCS

Bivalves

In the bivalves the shell encloses a molluscan body. Both shell and soft parts are in most cases symmetrical about the plane of the junction of the two valves, whilst each valve is generally asymmetrical about its median plane (a situation which contrasts with that of the brachiopods, see above). As in all molluscs, bivalves have a body with gut and pairs of gills and a strong muscular foot suspended in the space between the valves (the head having atrophied). These organs are enveloped by lobes of mantle tissue which line the inside of the two valves and are responsible for their secretion. The mantle margin has also taken over the sensory activity of the head providing an early warning system against attack or disturbance and triggering the closure of the valves.

The bivalve shell is variable in shape, and differences between genera can be understood in terms of modifications to the basic body structure as a consequence of the habitat of the animal. Most bivalve genera today are either infaunal (i.e. living wholly or partly in the sediment) or semi-infaunal, evidently as a protection against predators and also against being washed away by currents. These bivalves need to maintain a connection to the sediment surface for respiration and, in some cases, feeding. To facilitate this, the mantle margins are extended into two tubes (siphons), at the posterior end of the animal, and the shell may be elongated in this region to house these organs. Infaunal bivalves may also possess a strong foot which can be extruded from the shell to dig into the sediment. Sometimes the foot is so large that the shell cannot close properly at the anterior end, so forming a permanent gape. Instead of anchoring themselves in the sediment, other bivalves attach themselves to a firm substrate, in the case of oysters by cementing one valve to the substrate. Mussels also attach themselves, but using a bundle of small proteinaceous threads, called a byssus, which is secreted from just behind the foot.

Whilst generally rare in the Solnhofen Plattenkalk, most bivalves were of the cementing, or byssally attached variety. Many are juvenile oysters of the genus *Liostrea* (fig. 5.4, p. 78), but some are probably *Inoceramus*. They were attached to objects such as seaweed, twigs, bits of driftwood, belemnite rostra and the shells of ammonites which drifted into the lagoon. When the floats sank to the bottom of the lagoon the bivalves died and, after detachment, became scattered. In some cases the remains of the presumed float are no longer preserved, but its presence is inferred from the accumulation of small isolated shells in the sediment (see palaeoecology, p. 76). Some *Liostrea* reached quite large sizes (up to 70 cm) and must have drifted for a long time. More frequently the oysters were carried into the hypersaline waters and killed before they reached maturity. Of the other bivalves, a much greater diversity (although not numerical abundance) is found in the Kelheim area. There have been isolated finds of scallops, such as *Eopecten* (which was probably free-living as are modern scallops), or relatives of the present-day mussel, such as *Arcomytilus*. The narrow, triangular *Pinna* was suited to a semi-infaunal life partially buried in lime sand, whilst *Solemya* was a shallow burrower and survived sufficiently long in the lagoon to produce the trace fossils (see figs. 5.8 & 5.9, pp. 81–2).

A single specimen of the smooth, inequivalved *Buchia* has been found and this is of special significance. *Buchia* is a common genus in Jurassic sediments of the cooler northern seas. Its occurrence suggests that the Solnhofen lagoon was also connected to this northern province as well as to the southerly Tethys Ocean.

Gastropods

The soft body of the gastropod is similar to that of the bivalve in that the foot, gut, gills and other organs are associated with folds of mantle tissue. However, in gastropods the head is well developed and, instead of a predominantly bilateral symmetry, in most cases the body is coiled in a spiral. The body is housed inside a spiral, conical shell which usually is not partitioned into chambers as are cephalopod shells. The gastropod has a strong, muscular foot used to grip the substratum. As in bivalves, gastropods may have siphons which connect the mantle cavity to the external environment. Siphons or no, the shell aperture often has projections or indentations to channel water currents into the shell.

Gastropods of Late Jurassic times were both numerous and diverse, particularly in reefal environments, and they are well represented in the Solnhofen collections. There are low cones of the limpets *'Patella'* and the fat spirals of *Globularia*. Very occasionally numerous specimens of the gastropod *Spinigera* are found scattered over bedding planes in the Eichstätt area. This narrow cone has an elongate aperture and two spines per revolution of the shell. Many specimens attributed to the similar genus, *Rissoa*, together with their trace

fossils (see figs. 5.10 & 5.11, pp. 83–4), have been found on bedding planes in the Gungolding–Pfalzpaint area. This gastropod also has a narrow tight spiral of six to eight whorls, but a smooth shell. *Rissoa* lives today predominantly in the intertidal zone on the seaweed upon which it feeds. The Solnhofen representatives may have been carried into the lagoon on torn pieces of algae which are no longer preserved.

Cephalopods

Cephalopods are the most advanced of the molluscs, possessing the same basic arrangement of organs but with a particularly well-developed head and sensory organs. Primitively they all possessed an external, chambered shell. Modern cephalopods are conveniently subdivided into two groups. Those with four gills in the mantle cavity (known technically as the tetrabranchiates) and, incidentally, an external skeleton, are represented by the nautiloids, together with their fossil relatives, the ammonoids (presumed to have a similar soft-part morphology). Squids, cuttlefish and their fossil relatives, the belemnites, form the second group because they have, or are thought to have had, two gills in the mantle cavity (dibranchiate) and also an internal skeleton.

Squids and cuttlefish

The squids and the cuttlefish are amongst the better known of the modern dibranchiates. They may reach very large sizes; some modern giant squids have been measured at 18 m in length. Modern dibranchiates have some of the most highly developed nervous systems amongst invertebrates. Their sensory ability, co-ordinated with rapid movement, enables them to escape predators and to hunt on their own account. They move by a sort of jet-propulsion. The mantle sac, which lies underneath the head, is inflated with water which is then expelled rapidly through a funnel-shaped aperture to propel the animal backwards at some speed. A further device used by some squids to escape a would-be predator is the ink sac which may be discharged at an appropriate moment to confuse an attacker. In the Solnhofen Plattenkalk this ink sac is sometimes fossilized. Squids (fig. 7.14a) and cuttlefish (fig. 7.14b) are armed with ten tentacles, two of which are longer than the rest. These latter tentacles are retractable and have club-shaped ends, whereas the other tentacles have suckers. Fins along the side of the body control the direction of swimming. The internal skeleton is in the form of an elongate plate, and is a relatively common fossil in the Solnhofen Plattenkalk.

Plesioteuthis (fig. 7.15) is the most common Solnhofen squid and its cuttle-bone reaches 30 cm in length in the adult. Usually the cuttlebone is squashed laterally so hiding the small stabilizers that were present at its end. At the opposite end of the cuttlebone are traces of the ring of tentacles which were impressed into the sediment as the animal touched down on the seafloor.
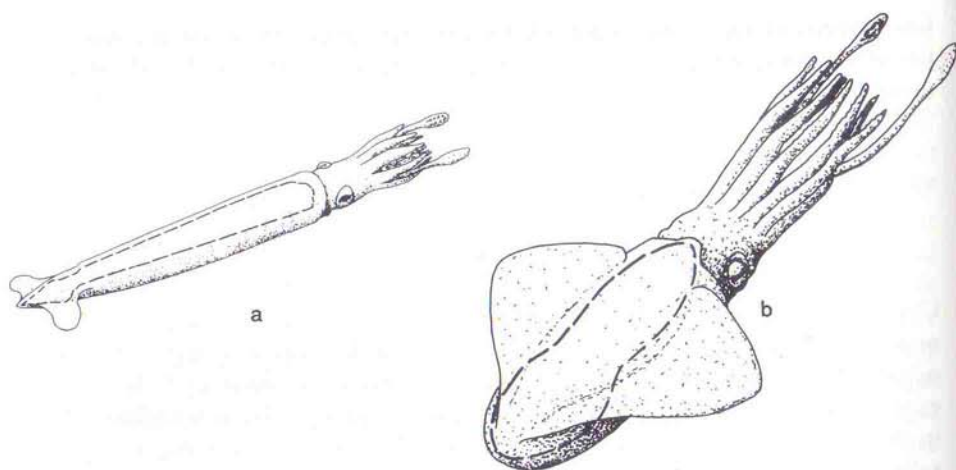
Fig. 7.14 Drawing of modern squid (a) and cuttlefish (b) showing position of internal skeleton.

Adjacent to the tentacles there are impressions of the jaws and mouth. Some phosphatization of the soft parts has occurred with the strong striations above the cuttlebone, on the back of the animal, apparently representing muscle fibres. The ink sac is the button-like organ in the middle of the body. *Trachyteuthis* (fig. 7.16) has a particularly sturdy blunt-ended cuttlebone up to 75 cm in length, with stabilizers towards the back. The underside of the cuttlebone is covered by a granular ornamentation in its central portion. The
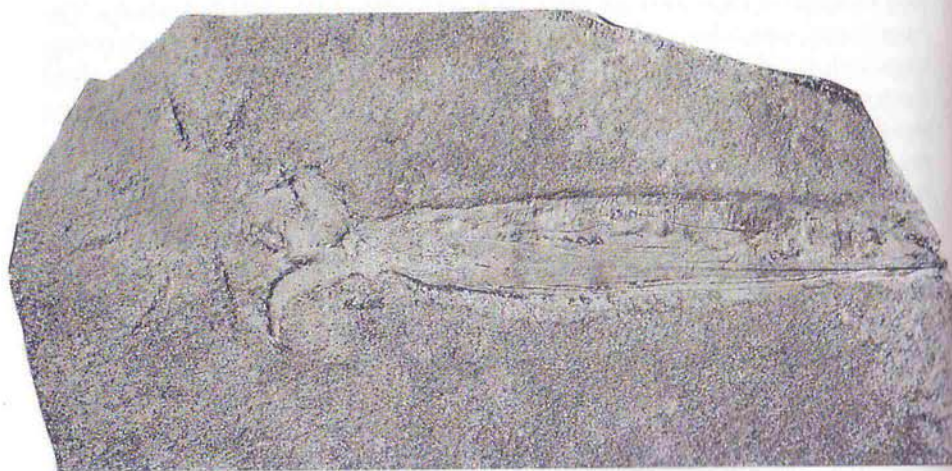
Fig. 7.15 Squid; *Plesioteuthis prisca* Rüppell, Blumenberg bei Eichstätt; preserved length of animal 256 mm; BSPHGM 1959 I 395.

soft parts of *Trachyteuthis*, known from other specimens, show that the animal possessed long, narrow tentacles and broad fins which ran the length of the beast.

Belemnites
The belemnites are an extinct group of dibranchiates whose internal skeleton is
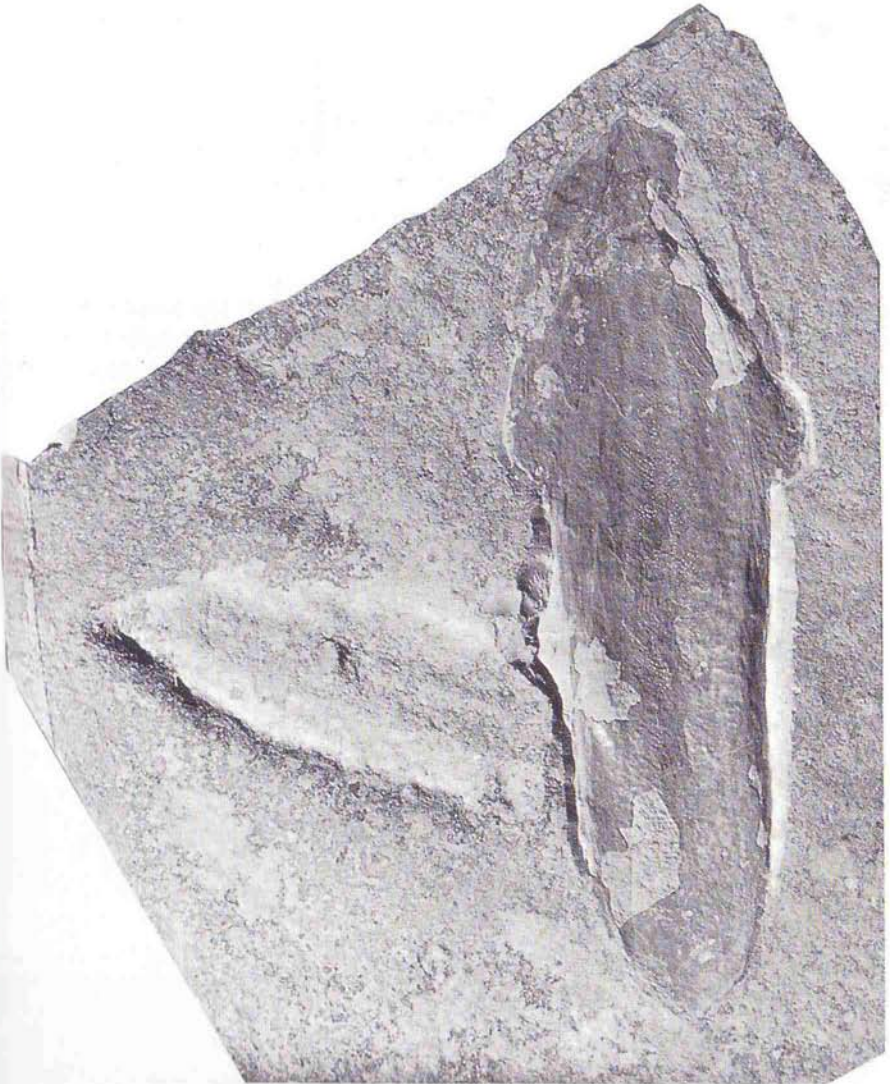
Fig. 7.16 Cuttlefish; *Trachyteuthis hastiformis* Rüppell, Solnhofen; cuttlebone length 310 mm; BSPHGM 1973 VII 60.

a common fossil in Mesozoic rocks. The main element of the fossils is the bullet-shaped guard, made of solid calcite, which lay somewhere in the back of the body, perhaps acting as ballast (see reconstruction of the living animal, fig 7.17). Inside the guard fitted the less easily fossilized, aragonitic phragmocone, conical in shape with a series of air-filled chambers. In the juvenile stages, when the guard was still relatively small and light, the phragmocone could have been used for regulating buoyancy (as in the nautiloids and ammonites). A thin fragile extension, the pro-ostracum (which resembles a cuttlebone) projects from the front of the phragmocone.

The most common of the Solnhofen belemnite remains are the guards of **Hibolites** (fig. 7.18). Juveniles predominate, and they are also very common in the underlying Treuchlingen marble (see p. 28). The fossil *Acanthoteuthis* was originally thought to be the disarticulated soft parts of *Hibolites* but it is now recognized as another squid (Engeser & Reitner 1981).

Nautiloids

Of the ammonites and nautiloids, abundant for much of the fossil record, the sole living survivor is *Nautilus*. The shells, which are often coiled, are subdivided by partitions (septa) into a series of chambers. The animal lives inside
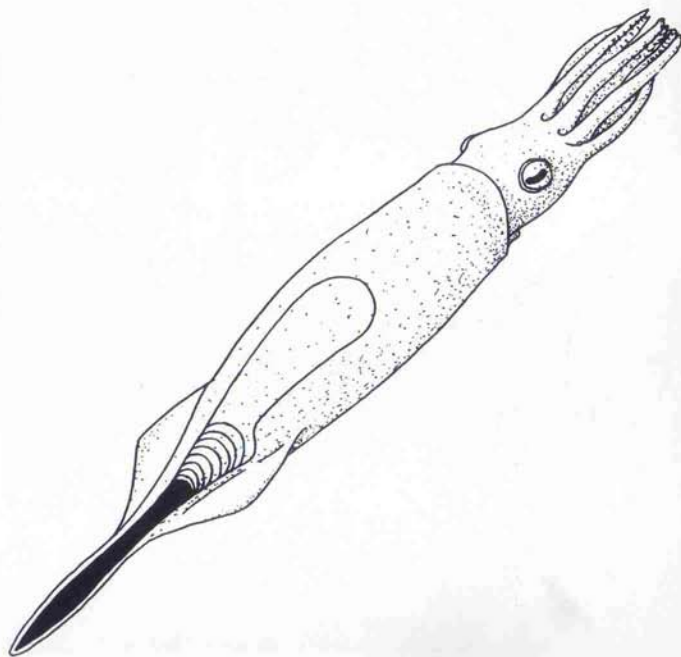
Fig. 7.17 Reconstruction of belemnite animal showing proposed position of belemnite as an internal skeleton.
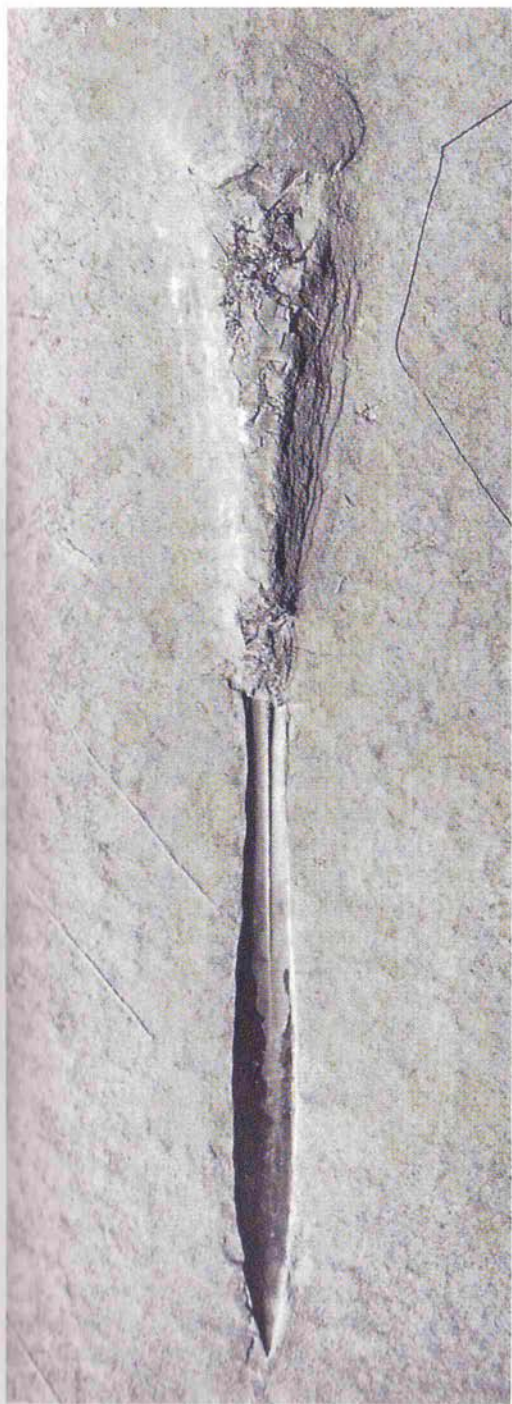
Fig. 7.18 Belemnite; *Hibolites hastatus* (Blainville), Solnhofen; total length 176 mm; BSPHGM AS VII 498.

the last chamber but maintains a connection with the inner chambers through a filament of living tissue inside a canal, a structure known as the siphuncle. In nautiloids the siphuncle passes through the centre of the smooth, disc-shaped septa, which are convex away from the aperture.

Being made almost entirely from aragonite, nautiloid shells, like those of ammonites, preserve poorly and, indeed, the Solnhofen nautiloids are scarcely recognizable. Only one genus, *Pseudaganides*, can be identified with any degree of certainty, and this is because it is also known from the Mörnsheim beds (p. 37) where silicified specimens are preserved in three dimensions. *Pseudaganides* has a tighly coiled, smooth shell which is slightly compressed in cross-section.

Ammonites

Jurassic ammonites have coiled shells with septa that are thrown into complex folds where they meet the shell margin, so making the typically ornate pattern of ammonite suture lines. Another feature which distinguishes them from the nautiloids is the position of the siphuncle, because it is displaced from the centre of the septa towards the outside of the whorls. The name ammonite, incidentally, comes from the name of the Egyptian god Amun-Re or Ammon, whose symbol, the coiled ram's horn, resembles the fossil shell. The ammonite animal, as reconstructed in fig. 7.19, is thought to have been similar to *Nautilus*.

Poorly preserved in the Solnhofen Plattenkalk, most ammonites are present as paper-thin impressions, sometimes lined by the outer organic membrane, known as the periostracum. Occasionally, the siphuncle is preserved as a thin black line, a consequence of its original phosphatic constitution. In most deposits the aptychi, calcareous plates located in the head region, fell out of the shell and were not preserved near to the rest of the ammonite. However, a large number of the Solnhofen ammonites are preserved with aptychi inside the body chamber (and being calcitic the aptychi preserve very well). The function of the aptychi in the ammonites is not known for certain. In some genera the
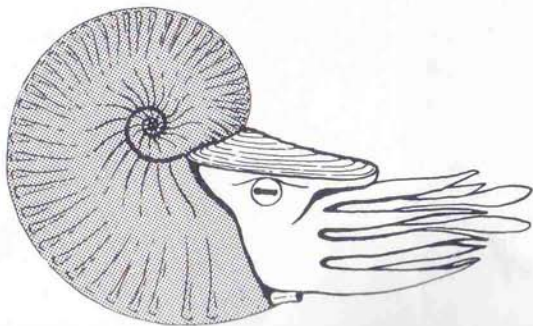
Fig. 7.19 Reconstruction of *Taramelliceras* animal.

two triangular plates may have formed part of the lower jaw although some palaeontologists consider that they were protective covers for the body chamber.

Ammonites are important as the zone fossils which help to date the Solnhofen Plattenkalk and the Mörnsheim beds (see fig. 2.13, p. 35, for drawings of these ammonites). The Solnhofen formation lies in the zone of *Hybonoticeras hybonotum* (Oppel), although the species itself is rare in the Solnhofen Plattenkalk. The illustrated specimen (fig. 7.20) is not very well preserved, but does have its aptychi, and is also encrusted by oysters. *H. hybonotum* has loosely coiled whorls without much overlap (a condition referred to as evolute), with rows of spines on both the inner and outer sides connected by strong ribs. Along the outer margin of the whorl runs a furrow, which is bordered by rows of small knobs. Although *H. hybonotum* is the zone fossil for the upper part of the Lower Tithonian (ti$_2$) in southern and central Europe (Tethyan province), it is not present in northern Europe (Boreal province) where beds of this age are characterized instead by the genus *Gravesia*. Significantly, southern Germany, being in an intermediate geographical position between both provinces, has both *Hybonoticeras* and *Gravesia*. *Gravesia* is generally larger than *Hybonoticeras*, reaching a diameter of 30 cm, and the whorls are evolute and quite broad in cross-section. On the inside of the whorls are coarse ribs which may divide into two or three towards the outer margin.

A further two species of ammonite are restricted in range to the Upper Solnhofen Plattenkalk and younger beds, and these are fairly common in relation to other Solnhofen ammonites. *Taramelliceras prolithographicum* (Fontannes) (fig. 7.21) is up to 10 cm in diameter with a fairly narrow aperture and a semi-involute shell. Ornamentation consists of slightly curved, sickle-shaped ribs on the flank of the whorl, with pronounced knobs towards the outside. *Glochiceras lithographicum* (Oppel) (fig. 7.22) is smaller, reaching a maximum diameter of 6 cm. Its whorls are narrow, but more evolute than *Taramelliceras* and are ornamented on the outer flank with pronounced sickle-shaped ribs, ending in knobs. Towards the inside of the whorl there are strong, broadly spaced and forward-inclined ribs. The aperture of *G. lithographicum* has a spoon-like projection at mid flank. *Neochetoceras steraspis* (Oppel) (fig. 7.23) is another of the common ammonites and is up to 15 cm in diameter. The aperture is narrow and the inner whorls are successively enveloped by the preceding ones (involute form), giving the shell a discoidal shape. (The involute form is not clear from the illustration because the siphuncle of the inner whorl is very prominent, giving a pseudo-evolute appearance.) External ornamentation is weak although most specimens exhibit some crescentic ribs which end in knobs towards the outside of the whorl. In contrast, the genus *Aspidoceras*, instead of being a flat coil is almost spherical in shape with a flaring aperture. Whereas some specimens lack ornamentation and have smooth

Fig. 7.20   Ammonite; *Hybonoticeras hybonotum* (Oppel) with *'Laevaptychus'*, Soln-hofen (?Eichstätt); maximum diameter 147 mm; BSPHGM AS I 566.

shells, others have a series of paired spines. *Aspidoceras* shells were often embedded vertically in the Solnhofen sediment and specimens are always broken.

The calcitic aptychi are fairly common, and there are three different types. Those belonging to the genera *Neochetoceras*, *Taramelliceras* and *Glochiceras* have a pronounced lamellate ornamentation and are thus termed Lamellaptychi (see fig. 7.23). Finely stippled aptychi are found inside the shells of *Aspidoceras* and *Hybonoticeras* and are called Laevaptychi (fig. 7.20), whilst more coarsely pimpled aptychi, Granulaptychi, belong to many of the ammonite genera with dividing ribs.

ARTHROPODS

Crustaceans

The crustaceans, together with the chelicerates and the insects, have traditionally been united under the title of Arthropoda. All arthropods are bilaterally symmetrical, segmented animals with a hard exoskeleton often mineralized by calcium salts or phosphatic compounds. In crustaceans the body is divided into a head, thorax and abdomen. The head bears five pairs of appendages, specialized as antennae and as mouth parts, whilst each thoracic and abdominal segment typically bears one pair of appendages which are used mainly for walking or swimming. Sometimes, however, the abdominal appendages are reduced or even lost. Often a fold of the exoskeleton, the carapace, extends back from the head to cover some of the thoracic segments.

Malacostracans

These are the best known Crustacea of today and include the gastronomically acceptable lobster and langoustine. The exoskeleton is fairly well calcified, so the forms are well preserved as fossils in the Solnhofen Plattenkalk. Typically they have a carapace and small tail fin (telson).

In the **mysidaceans**, such as the unfigured *Francocaris*, the carapace covers most of the thorax, and the abdomen is long and thin. The eyes are on movable stalks on the front of the head. **Isopods**, of which *Urda* (again unfigured) is one, are flattened dorso-ventrally and do not possess a carapace. The wide thoracic segments are fairly short and unspecialized and the first is fused to the head. The abdomen is short and the last abdominal segment is included in the telson.

The **Decapoda** comprises a diverse group and includes today's prawns, lobsters and crabs. It accounts for the majority of the Solnhofen crustaceans. The carapace is fused dorsally to all thoracic segments and extends laterally. Of the thoracic segments the first three help to form the jaws and the next five have walking legs, one or more terminating in a pincer. Each of the well-developed abdominal segments has a pair of swimming legs, with the last pair helping to form the tail. The **shrimps** are the most numerous of the Solnhofen decapod

Fig. 7.22 Ammonite; *Glochiceras lithographicum* (Oppel), Mörnsheim beds, Mörnsheim; maximum diameter 46.5 mm; BSPHGM 1959 XI 50.

crustaceans. In shrimps the first three pairs of walking legs terminate in pincers. The carapace is either cylindrical in shape or somewhat laterally compressed and is adorned with a long spine which reaches forward over the eyes. The second pair of antennae is typically very long. In *Aeger* (fig. 7.24) the carapace is slightly laterally compressed. The front pair of legs is of the same length as the following two, but bears comb-like bristles. In **reptantians**, which include the crayfish, crabs and lobsters, the carapace is cylindrical or dorso-ventrally flattened. The first three pairs of walking legs have pincers, the first pair of which is the largest. *Mecochirus* (figs. 7.25, 7.26 & 5.12, p. 85) is the only relatively common fossil representative of this group in the Solnhofen Plattenkalk. It has a very long and strongly calcified front pair of walking legs by which it levered itself up out of the sediment and so swung its body backwards. Marks of these legs may be seen in its trace fossil. The crab-like *Cycleryon* (fig. 7.27) has a flattened, sub-circular carapace with a toothed margin at the front and a granulate ornamentation on the top. The antennae are short. The figure shows the underside of *Cycleryon* with its large first pair of walking legs. The first four pairs of walking legs have narrow pincers. The first abdominal segments have a ridge running down the middle and the tail fan is made of triangular sections. *Cancrinos* (fig. 7.28) is a true crab because its abdomen is curled under the body and acts as an additional appendage. It is stoutly built with a short carapace

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Fig. 7.21 Ammonite; *Taramelliceras prolithographicum* (Fontannes), Mörnsheim beds, Mörnsheim; each ~45–60 mm diameter; BSPHGM 1959 XI 48.
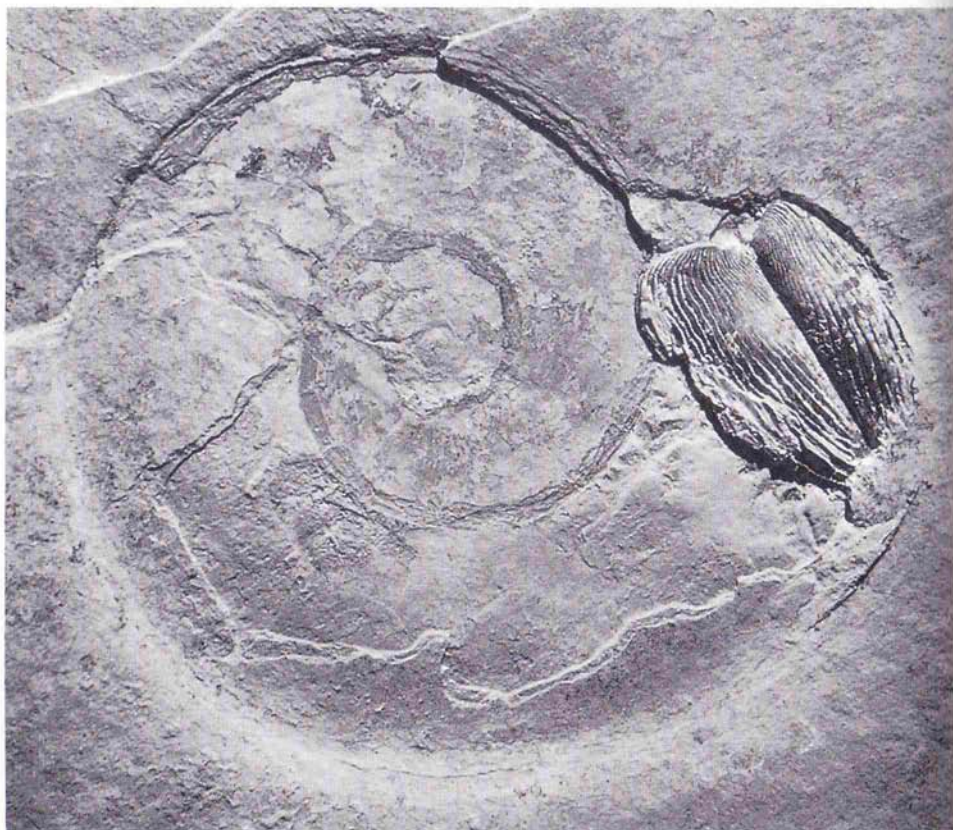
Fig. 7.23   Ammonite; *Neochetoceras steraspis* (Oppel) with *'Lamellaptychus'*, Solnhofen; maximum diameter 138 mm; MSAV.

bearing a granulate ornamentation. The walking legs are large, without pincers, and the second pair of antennae are large and club-shaped. *Magila* (figs. 7.29 & 7.30) is a small, weakly calcified, burrowing form with a broad, first pair of walking legs and a small second pair, both with pincers. The carapace has a furrow between the portions which correspond to the head and the thorax. Both antennae are well developed.

Another group of malacostracan crustaceans, although far less diverse than the decapods, is the **stomatopods**, or mantis shrimps. *Sculda* (figs 7.31 & 7.32) is a rare genus with a compact, broad body. The segments at the back have a comb-like edge and are ornamented with short gills. The eyes are on stalks.

Fig. 7.24 Decapod crustacean; *Aeger tipularius* Schlotheim, Eichstätt; carapace length 31 mm; private collection.

Ostracods

These millimetre-size crustaceans are encased in a bivalved carapace which is hinged about the animal's back, so that it superficially resembles a very small bivalved mollusc. The soft bodies of living ostracods show a head unpartitioned from the rest of the body and very small, but highly specialized limbs. Unfortunately, Solnhofen ostracods are poorly preserved and show no details of the soft parts. The calcareous carapaces are either smooth with a short protuberance on the side of the valve opposite the hinges, or else weakly pitted and lacking this bulge (see also p. 46).
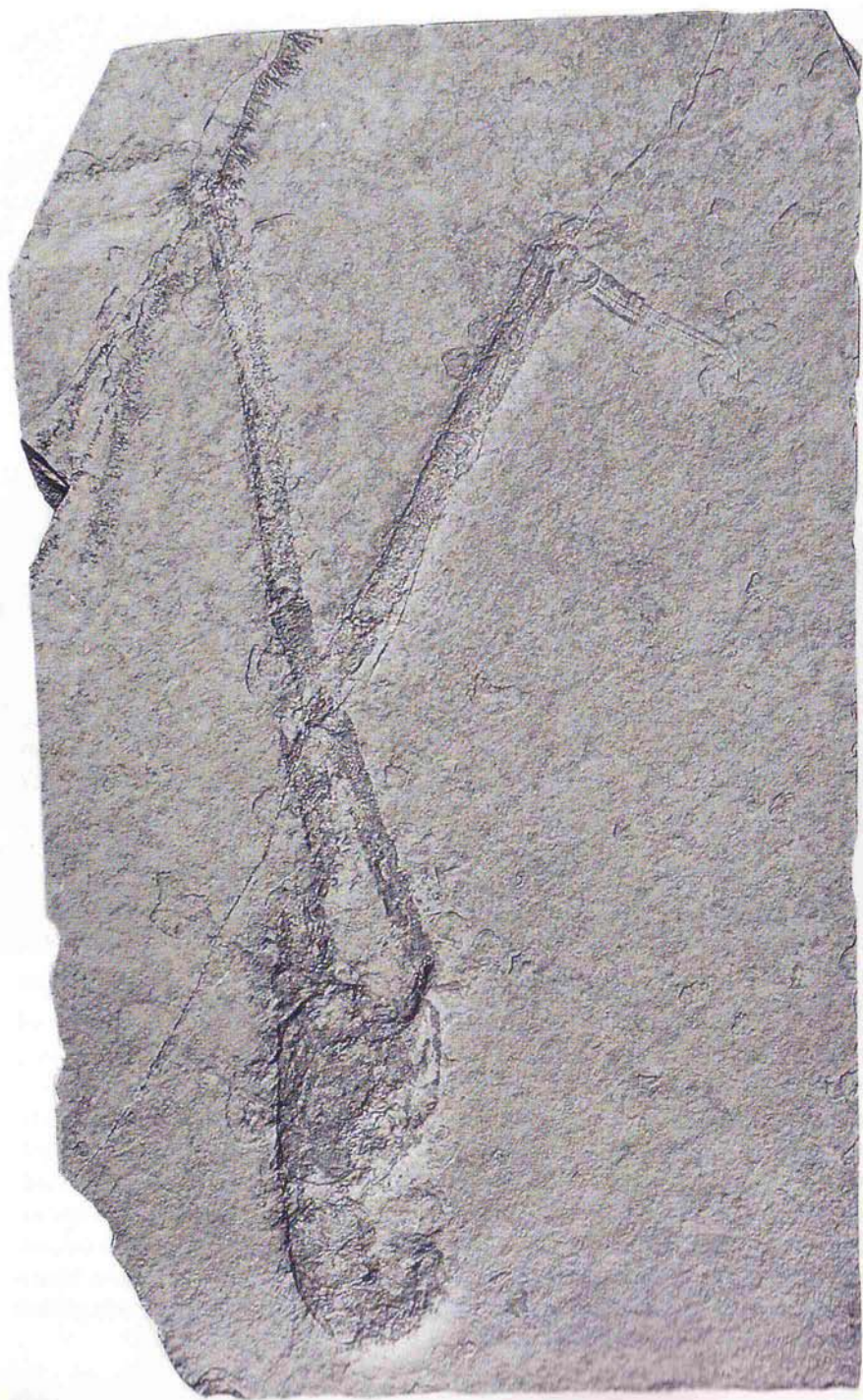
Fig. 7.25 Decapod crustacean: *Mecochirus longimanatus* (Schlotheim), Eichstätt; length 198.5 mm; PAMNHUB 1974.17.1.
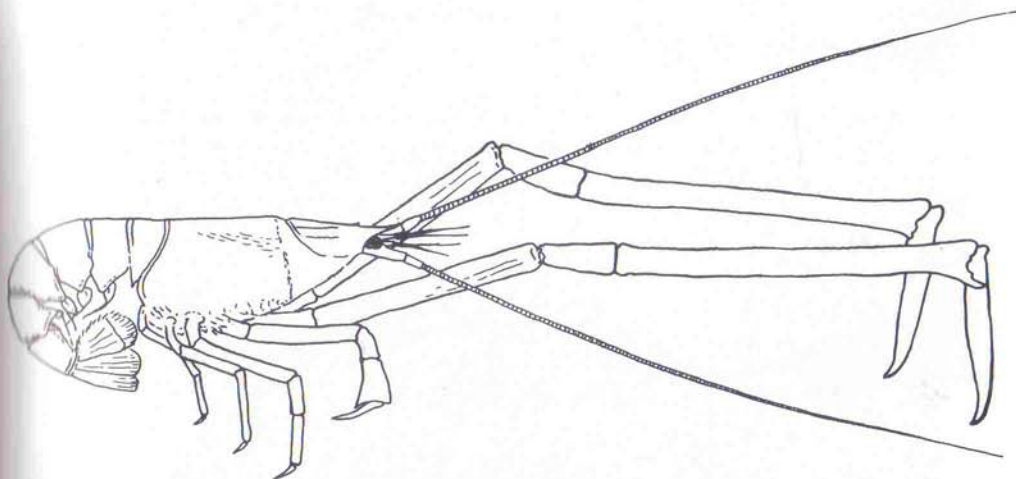
Fig. 7.26   Drawing of *Mecochirus*.

Barnacles (cirripedes)

Barnacles are crustaceans in which a free-living larval stage precedes the sessile adult. Barnacle larvae settle on hard substrates and, lying on their backs, comb the water with their legs, picking out suspended food particles. One group, that includes the Solnhofen genus *Archaeolepas*, has a small body armoured by strong calcite plates and sits on an elastic stalk. A colony of this genus is known from the Solnhofen Plattenkalk, and this was carried into the lagoon on an ammonite shell (figs. 7.33 & 7.34). Other barnacles form a home by boring into the shells of other invertebrates (although the association is not truly parasitic). The slit-like openings of these excavations made by the barnacles have been observed on belemnites from Daiting and are referred to by the trace fossil name of ***Brachyzapfes***.

Chelicerates

In chelicerates, the arthropod body is divided into an anterior and posterior section. The anterior section corresponds to a fused head and thorax, and the posterior section to the abdomen and tail. The first pair of the six thoracic appendages is small and bears pincers, the diagnostic chelicerae which give the group its name. The posterior section comprises the abdomen and the tail. Chelicerates encompass a wide group of organisms, including both the terrestrial spiders and the marine xiphosurans.
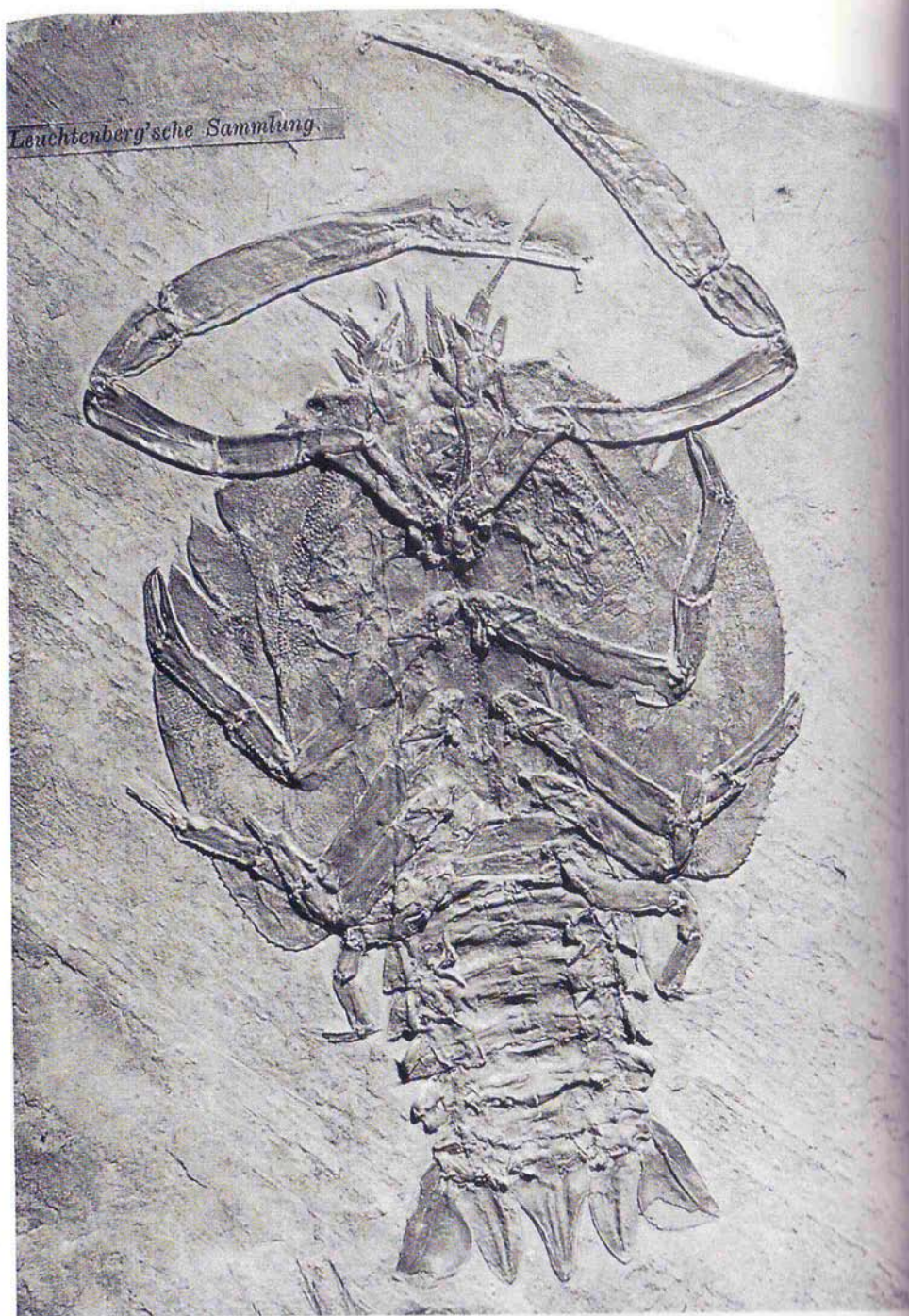
Fig. 7.27 Decapod crustacean; *Cycleryon propinquus* (Schlotheim), Eichstätt; total length 157 mm; BSPHGM AS V 31.
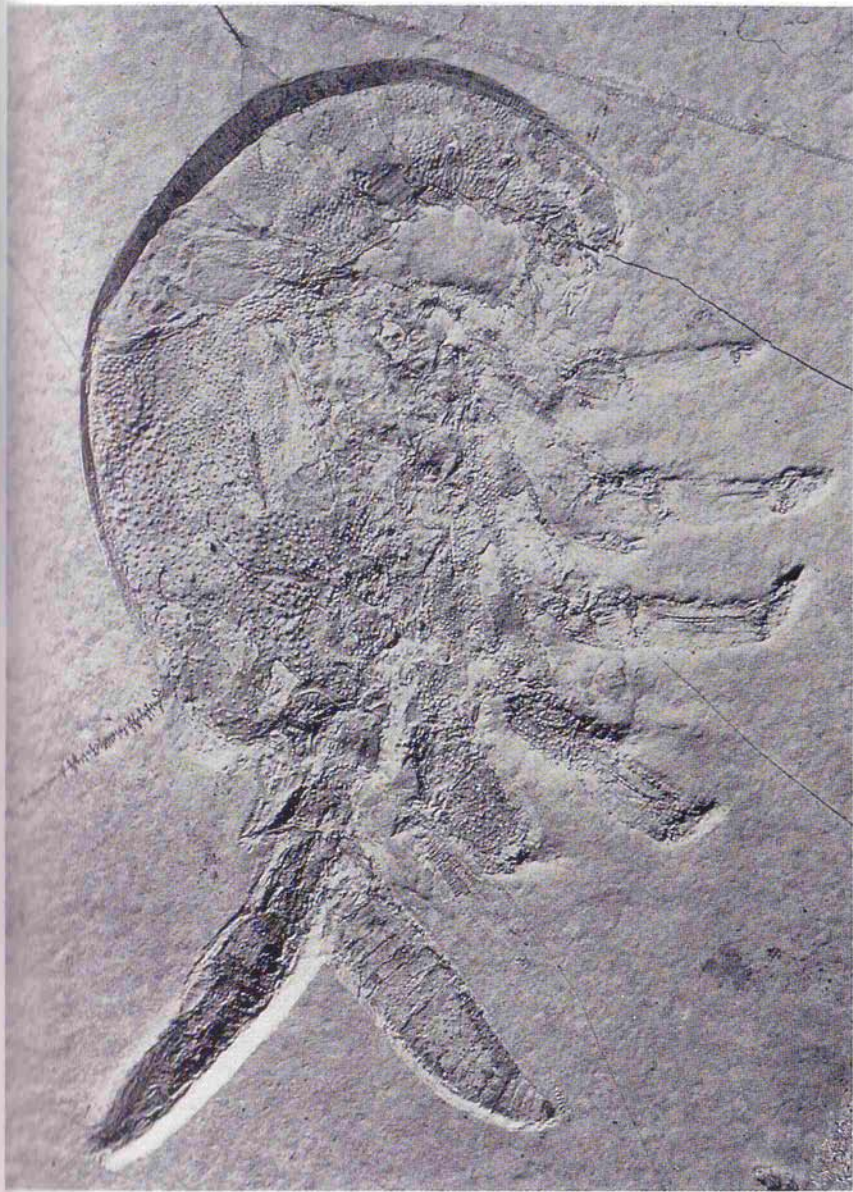
Fig. 7.28 Decapod crustacean; *Cancrinos claviger* Münster, Blumenberg bei Eichstätt; maximum distance from end of upper antenna to end of abdomen 209 mm; Museum Bergér, Harthof bei Eichstätt.

Fig. 7.29 Decapod crustacean; *Magila latimana* Münster, Schernfeld bei Eichstätt; total length 28 mm; BSPHGM 1964 XXIII 163.
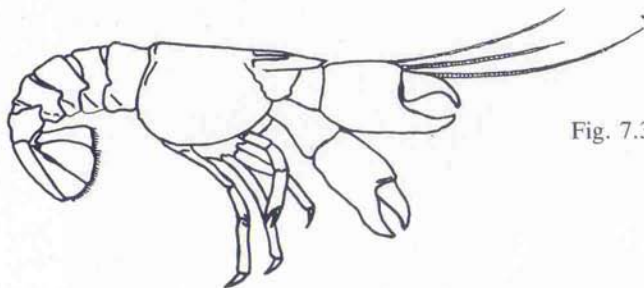
Fig. 7.30 Drawing of *Magila*.

Xiphosurans

The xiphosurans include one of the Plattenkalk's most famous fossils, **Mesoli-mulus** (fig. 7.35 and figs. 5.5 & 5.7, p. 78 & 80), a close relative of the modern horse-shoe crab *Limulus* (see fig. 5.6, p. 80). Today *Limulus* lives in shallow coastal waters and is found in great numbers on the east coast of North
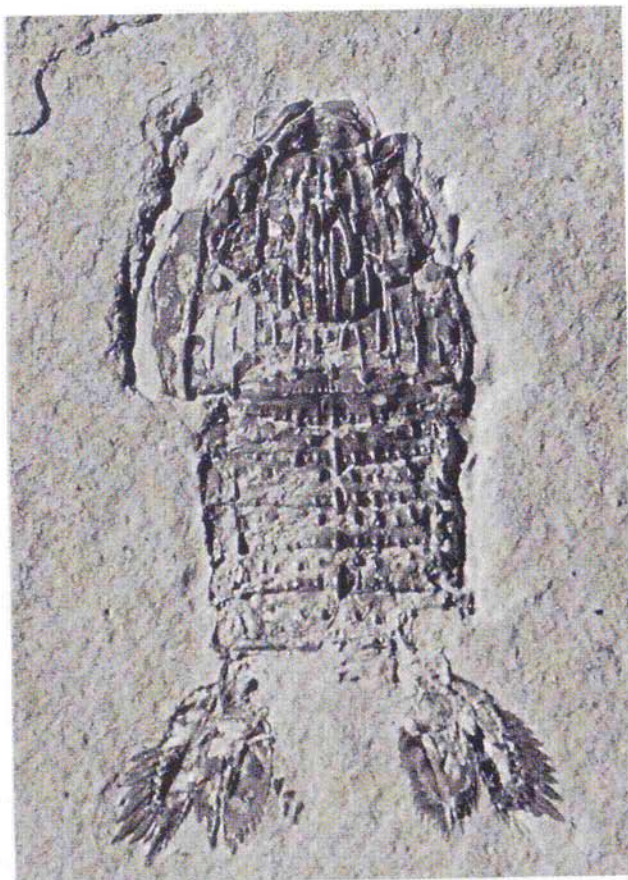
Fig. 7.31   Stomatopod crustacean; *Sculda spinosa* Kunth, locality given as Solnhofen but more likely to be Kelheim; total length 32 mm; BSPHGM AS I 812.
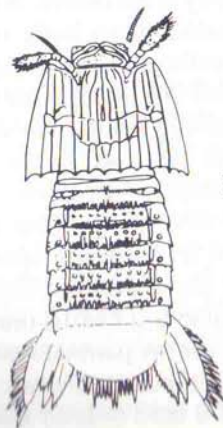
Fig. 7.32   Drawing of *Sculda*.

Fig. 7.33 Barnacle; *Archaeolepas redtenbacheri* (Oppel), Kelheim; ×2; BSPHGM AS I 806.

America, on some Pacific islands and in Japan. Limulids burrow in the mud to shallow depths in search of small invertebrates for food. They may spend short periods out of the water, and they are particularly tolerant to fluctuations in the salinity or temperature of the water. Consequently, it is not surprising that they were one of the few animals still alive when they reached the poisonous lagoon floor, being responsible for some of the famous spiral tracks or 'death marches' which terminate with the body at the centre. Some of the fossils are the remains of moulted exoskeletons rather than body fossils. In contrast to some of the crustaceans, limulid moults are almost impossible to distinguish from the body fossils. This is because the shell splits only along its anterior margin and the animal slips out leaving behind the intact, rigid exoskeleton with all its appendages. More about the trace fossils and activity of *Mesolimulus* in the lagoon is given in the chapter on palaeoecology (pp. 77–9).

Almost all fossil limulids from the western area of Solnhofen and Eichstätt are thought to be juveniles, a conclusion reached by comparison with much larger individuals from the reefal areas of Kelheim. *Mesolimulus* has a large carapace covering the head and front of the thorax, on the top of which are two kidney-shaped eyes. There are six pairs of limbs under the front of the body, the first bearing large pincers, the next five used for walking, the last of which has a brush-like ending and is used to lever the body forwards.

Fig. 7.34   Barnacle; *Archaeolepas redtenbacheri* (Oppel), Kelheim; ×2; BSPHGM AS I 807.

Arachnids

A rather dubious palpigrade is recorded from the Solnhofen Plattenkalk under the name of **Sternarthron**. Palpigrades are relatives of the spiders, but have legs which are fairly long and thin and a body which tapers to a flagellum. The body is a curious spindle shape and shows neither the swollen posterior nor the division between the anterior and posterior typical of modern spiders. Modern palpigrades live under stones and in crevices and are never greater than 3 mm in length. The Solnhofen example is nearer 20 mm in length, so if it is generally comparable to modern palpigrades it must have had a very different mode of life.

Insects

Insects are terrestrial arthropods, some of which have become adapted for a life in or around freshwater. They are the most diverse group of all living animals and they also account for the greatest proportion of species in the Solnhofen Plattenkalk. The body is divided into head, thorax and abdomen and these are strongly differentiated from each other. On the thoracic segments insects have three pairs of legs and often two sets of wings, whilst the head is adorned with a highly developed set of mouthparts and one set of sensory antennae. All the types of insects fossilised in the Solnhofen beds are those which possessed external jaws covered by upper and lower flaps of cuticle. Only winged insects are known, presumably because they were blown out into the Solnhofen lagoon (see also p. 86).
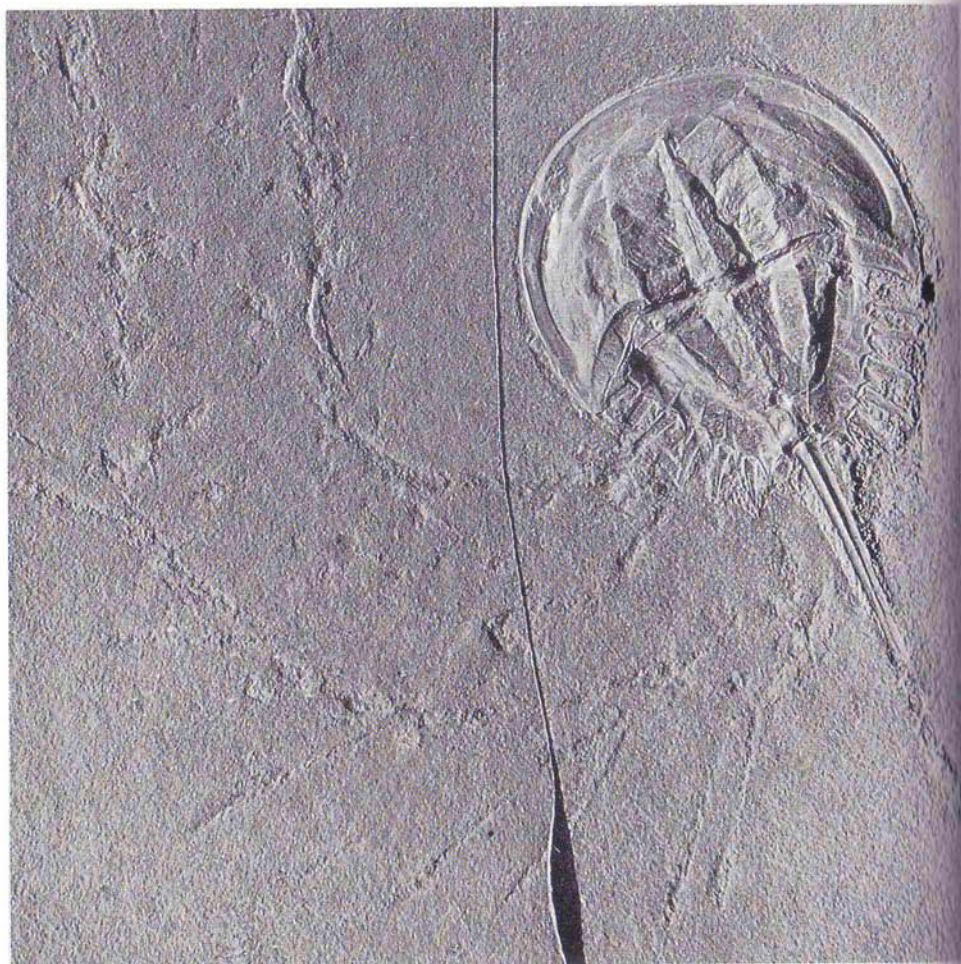
Fig. 7.35 Xiphosuran chelicerate; *Mesolimulus walchi* Desmarest, Maxberg bei Soln-
hofen; width of carapace 92 mm; MSAV.

The insects of Late Jurassic times were already fairly advanced and around
two-fifths of the modern orders are represented in the Solnhofen Plattenkalk.
Characteristics at the genus and particularly at the species level are often
difficult to determine because the preservation, which is mainly as impressions,
is not sufficiently clear. Most insects from the Solnhofen Plattenkalk have come
from the Eichstätt quarries and a few from the Solnhofen area.

Mayflies (Ephemeroptera)
Mayflies have narrow bodies, generally around 3 cm in length, with two long
tail hairs (fig. 7.36). The front pair of wings is large and the hind pair small. In
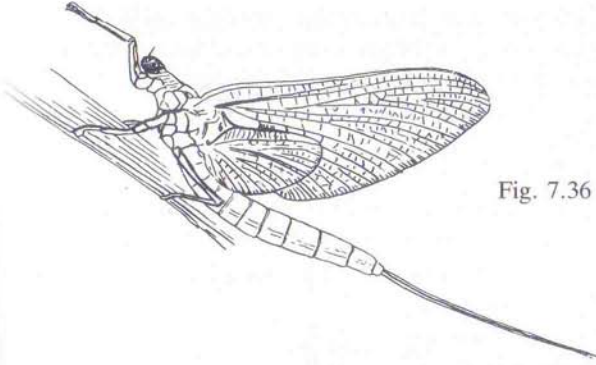
Fig. 7.36 Drawing of modern mayfly.

modern mayflies practically the entire life cycle is spent in the larval stage when the insects swim and feed on plants. The adult, when hatched, has only days, or even hours, to breed, lay eggs and die. The illustrated *Hexagenites* (fig. 7.37) is a typical example.

Dragonflies (Odonata)

Dragonflies are also dependent on freshwater for the larval stage. Dragonflies have a head with large, prominent eyes and short antennae. The thorax is short, whilst the abdomen is long and narrow, terminating in two short tail hairs. Two long, but narrow pairs of membranous wings with a vine venation are attached to the thorax. To accommodate the wings, the legs are shifted far to the front of the thorax. As the dragonflies are amongst the most aesthetically pleasing of the Solnhofen fossils, here two different genera are figured.
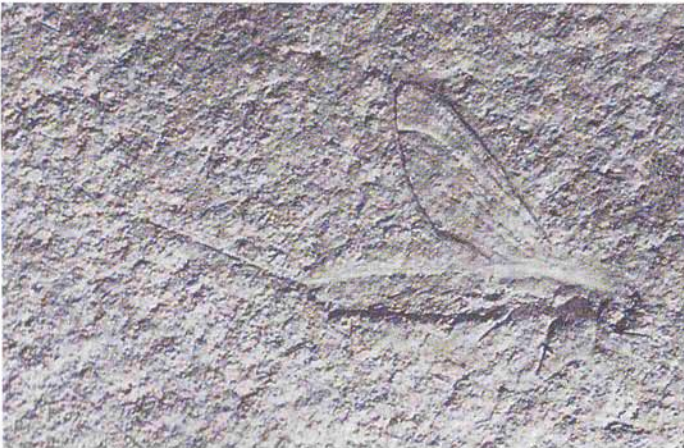
Fig. 7.37 Mayfly; *Hexagenites cellulosus* Hagen, Eichstätt; total length 52.5 mm; BSPHGM AS I 808.

Libellulium (fig. 7.38) has large, powerful wings which in the illustrated specimen are spread out, a common type of preservation. On this specimen the delicate venation is enhanced by the precipitation of dark iron oxide. In *Anisophlebia* (fig. 7.39) the wings are folded back over the body.

Cockroaches (Blattoidea)
The body is dorso-ventrally flattened and a shield covers the thorax and back of the head. The front wings are large and powerful with a characteristic venation, whilst the hind wings are small and delicate. In *Lithoblatta* (fig. 7.40) the wings are extended.

Water skaters (Phasmida)
The light body and long, splayed-out legs enable the creature to walk on the water surface. *Chresmoda* (fig. 7.41) may have lived in streams or on the surface of the lagoon or, as some modern forms, it might have been fully marine.
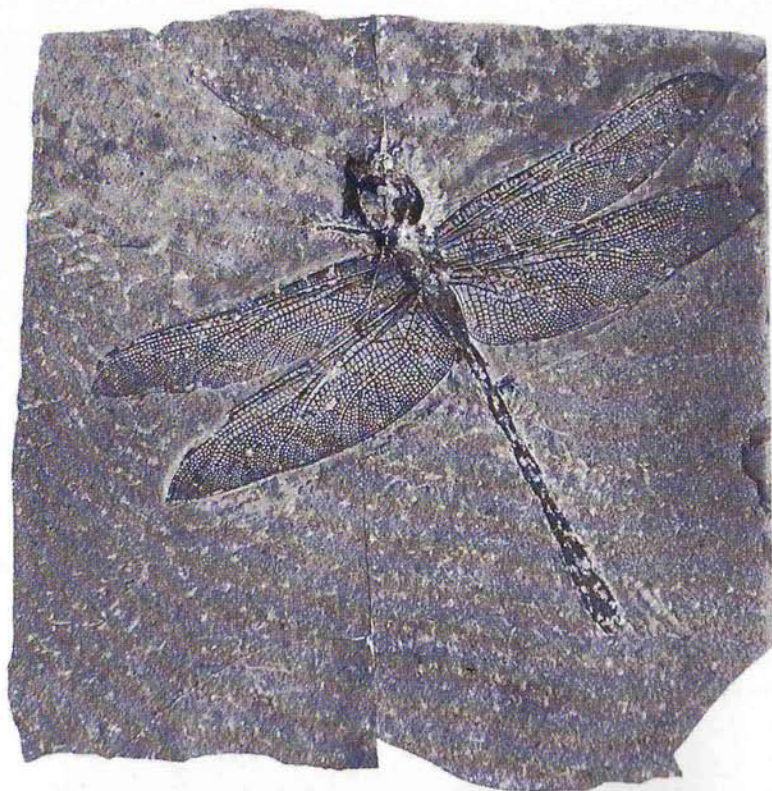
Fig. 7.38 Dragonfly; *Libellulium longilatum* (Germar), Eichstätt; maximum wingspan 138 mm; BSPHGM AS VI 36.
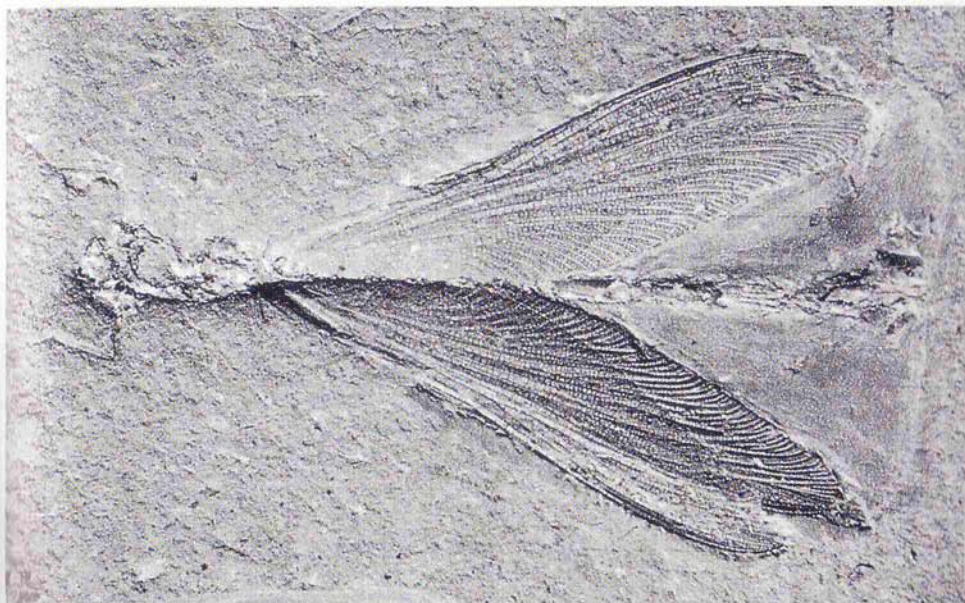
Fig. 7.39   Dragonfly; *Anisophlebia helle* (Hagen), Solnhofen; body length 92 mm;
BSPHGM AS I 804.

Fig. 7.40   Cockroach; *Lithoblatta lithophila* (Germar), Eichstätt; wingspan 35.5 mm;
BSPHGM AS V 33.

Fig. 7.41   Water skater; *Chresmoda obscura* Germar, Eichstätt; body length 49 mm; JME.

Locusts and crickets (Ensifera)

The ensiferans have particularly long hind legs which are well adapted for jumping. Their heads are large and the antennae are as long as the body, or longer in jumping forms. Burrowing forms are also known. The females are recognized by their long ovipositors, so we can deduce the figured specimen to be a male. A large number of the smaller insects are included as crickets under the label '*Elcana*', but their genus is difficult to determine owing to their poor preservation. *Pycnophlebia* (fig. 7.42) is the most common Solnhofen locust. The antennae, measuring some 13.5 cm, are longer than the body. As in nearly all ensiferan specimens, this one is laterally embedded and not very well preserved.

Bugs and water scorpions (Heteroptera)

The forewing is hardened and covers the membranous front half of the hind wing. The back is covered by protective shields, firstly a thoracic shield and then behind that a triangular field which is bordered by the underside of the partial wing cover. Both land and water forms exist, and even the water forms are excellent fliers. *Mesobelostomum* (figs. 7.43 & 7.44) is very similar to the giant American water scorpion (fig. 7.45), although it does not reach quite such

Fig. 7.42   Locust; *Pycnophlebia robusta* Zeuner, locality given as Solnhofen but is more probably Eichstätt; length along body and wing 121 mm; BSPHGM 1852 a 247.

Fig. 7.43 Water scorpion; *Mesobelostomum deperditum* (Germar), Eichstätt; body length 70 mm; BSPHGM AS I 538a.
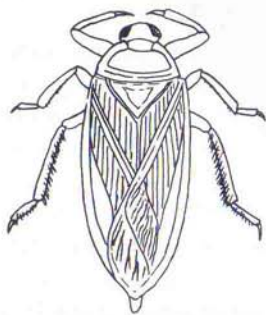
Fig. 7.44 Reconstruction of *Mesobelostomum*.
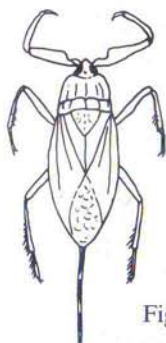
Fig. 7.45   Drawing of *Nepa*, modern American water scorpion.

an extreme in size (some modern forms of over 10 cm are known). Water scorpions live off young fish and other small water creatures. From time to time they climb to the water surface for air.

Cicadas ('Auchenorryhnchans')
The forewings are seldom strengthened to the extent of the hind pair. The wings, which may sometimes be quite wide and butterfly-like, are folded back over the body when not in use. The hind legs are long. A Solnhofen representative (not illustrated) is *Archepsyche*.

Lacewings (Neuropterans)
As in the beetles and wasps, both pairs of wings are of similar, large size, with long straight veins, interconnected by a system of thinner veins, although details of the venation vary between the wings. Some lacewings look fairly similar to the butterflies, but at rest lacewings fold the wings back over the abdomen, whilst in butterflies they remain clasped together and vertically erect. In addition the antennae are between the eyes rather than in front. *Kalligramma* (fig. 7.46) is the largest insect from the Late Jurassic. It is rather different from modern examples and so may have had a different life style. In this specimen, one of the forewings is not preserved.

Beetles (Coleoptera)
The chitinous integument of beetles makes a strong, protective armour. The front pair of wings form the strong wing-covers, or elytra, beneath which the hind wings are folded. Beetles have taken over many habitats, even freshwater. They are relatively common in the Solnhofen Plattenkalk, but unfortunately show few characters useful in their classification. In fig. 7.47 *Cerambycinus*, a possible relative of the modern wood beetle, is shown. Prominent is the square head of the beetle, the relatively short abdomen with large, granulate elytra, and the impressions of the long legs.
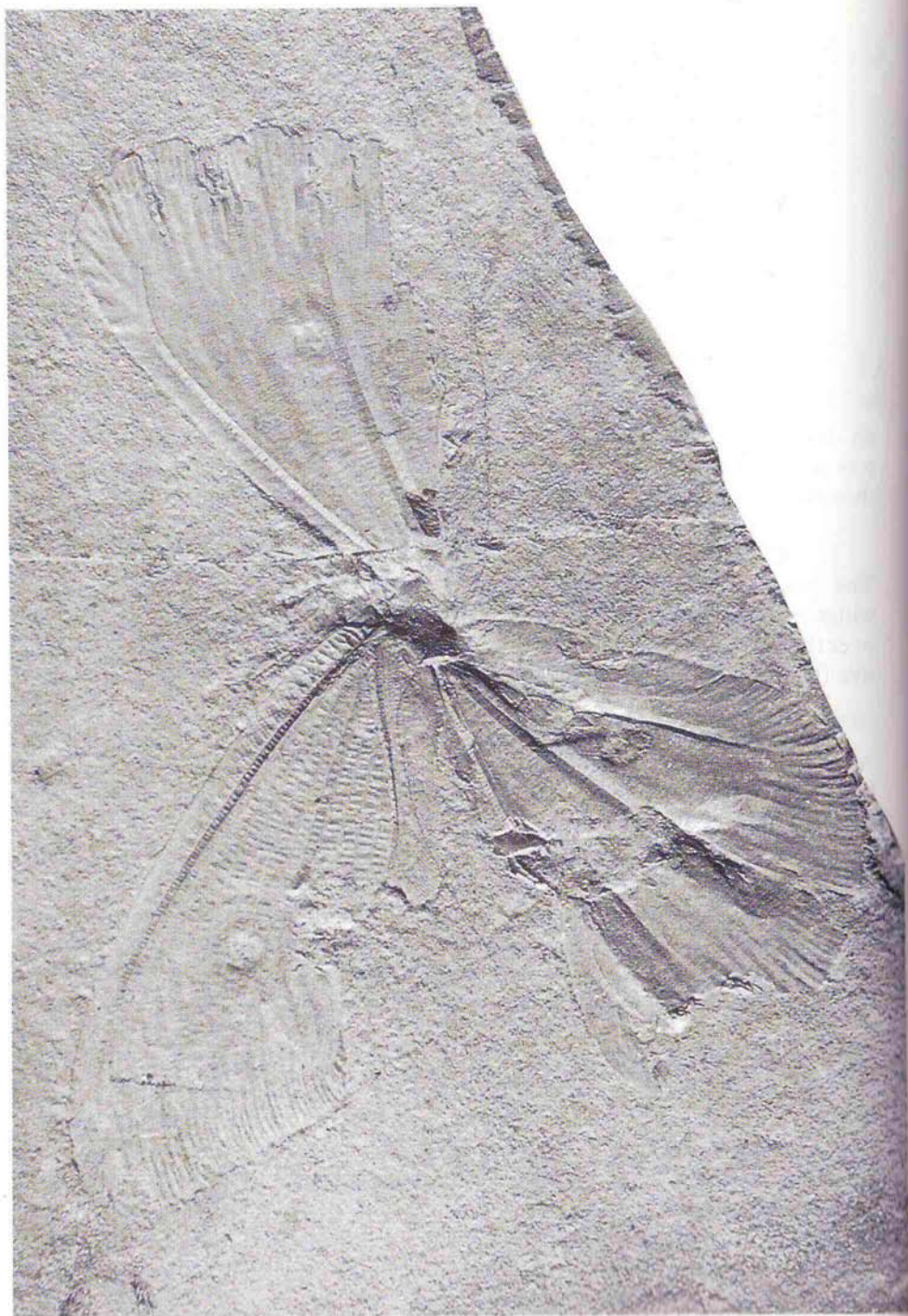
Fig. 7.47 Beetle; *Cerambycinus dubius* Germar, locality Solnhofen, or perhaps Eichstätt; body length 21.5 mm; BSPHGM AS VII 354.

Wasps (Hymenoptera)

Wasps are characterized by two membranous pairs of wings and the fact that the first segment of the abdomen is fused to the thorax. Females have a long, sharp ovipositor used for stinging, piercing or sawing. *Pseudosirex* (fig. 7.48) is thought to be a relative of the modern giant wood wasp, *Sirex*. The wood wasp females bore into dead trees, using their ovipositor spines, and lay their eggs inside. When the larvae hatch, they feed on the wood, which also shelters them. It is quite likely that the Jurassic wasps had similar habits. The illustrated example came to rest on its back, on what is now the bedding plane, and so the legs, which are inside the slab, are not visible. The long antennae are lost but the wing venation is excellently preserved.

Fig. 7.46 Lacewing; *Kalligramma haeckeli* Walther, Solnhofen; maximum wingspan 252 mm; BSPHGM 1902 I 6.

Fig. 7.48 Wasp; *Pseudosirex schroeteri* (Germar), Solnhofen; total length 80 mm; IGPTUB. Photograph by B. Kleeberg.

Caddis flies (Trichoptera)
The wings, which are very hairy, have only a few cross-veins. The three main veins in the posterior sector unite around the margin of the wing. The Solnhofen Plattenkalk has yielded such genera as **Archotaulius** and **Mesotaulius** (neither illustrated).

Flies (Diptera)
The hind wings are diminished to drum-like organs which swing during flight, acting as gyroscopes. The mouth organs are designed for piercing and sucking and the eyes are generally large. Classification of the Solnhofen flies is in need of revision. **Prohirmoneura** (not illustrated) is an example from the Solnhofen Plattenkalk.

ECHINODERMS

Echinoderms are a group of marine animals with a skeleton of porous calcite plates. Technically this is an internal skeleton, although in life the test is only covered by a very thin layer of soft tissue. On death the plates may disarticulate but, at least in the echinoids (sea-urchins), this happens very slowly and entire tests are quite commonly fossilized.

Echinoderms are characterized by a pentameral symmetry, although in some forms a bilateral symmetry has been superimposed. Openings in the test included a mouth and anus, usually on opposite sides of the skeleton, as well as pores for the protrusion of tube feet which help the animal to maintain a connection to the outside world from inside its calcite box. The tube feet are all interconnected and work on a hydraulic system, known as the water-vascular system. This is a diagnostic feature of all echinoderms. In outline, the system consists of a ring-shaped canal that connects to the seawater via a perforated pore on the top of the test. From this ring canal arise five major branches, terminating in the tube feet which protrude from the paired pores. The areas of the test containing these paired pores are termed ambulacra, whilst the rows of intervening plates are called the interambulacra. Both ambulacral and inter-ambulacral plates may be covered by spines.

Sea-lilies (crinoids)

The majority of crinoids in the fossil record are of the attached, sessile variety. A stalk anchors the main body of the animal, known as the cup (or calyx), to the substrate. The mouth projects upwards and is surrounded by five (or a multiple thereof) arms (ambulacra) which bear hair-like processes, known as the pinnules. Both arms and pinnules have tube feet which trap food particles. Only one genus of sessile crinoid (*Millericrinus*) is, however, recorded from the Solnhofen Plattenkalk, the remainder being free-swimming forms. In these latter forms, the stalk is either lost entirely or reduced to small movable processes that arise on the side of the calyx opposite to the mouth and ambulacra.

Saccocoma (figs. 7.49 & 7.50) is by far the most numerous not only of the crinoids, but of all the Solnhofen macrofossils. Specimens of *Saccocoma*, particularly the juveniles with calyces only a millimetre in diameter, are very common on some bedding planes in the Eichstätt area (see p. 90). The mature animal is not much bigger, not exceeding about 8 mm in diameter. Protruding from the calyx are ten ambulacra with pinnules which aided swimming. *Pterocoma* (fig. 7.51) is also a fairly common fossil, although not in comparison to *Saccocoma*, and many specimens have come from the Zandt and Eichstätt quarries. *Pterocoma* is much larger than *Saccocoma*, the arms being up to 10 cm in length and possessing long, delicate processes.
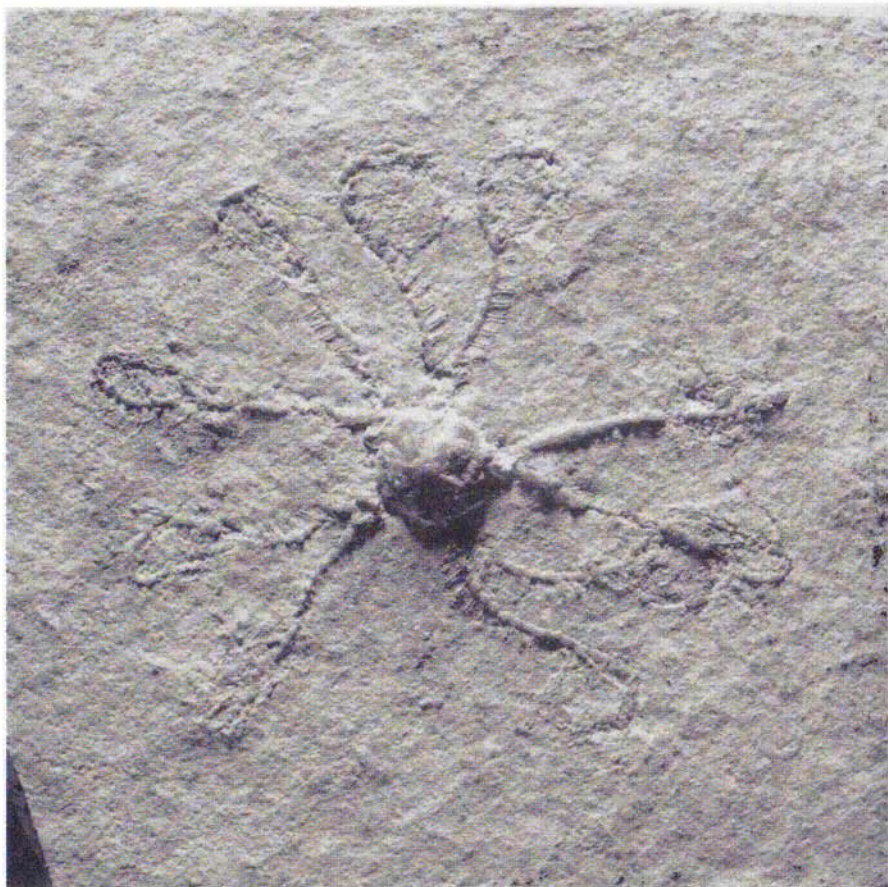
Fig. 7.49 Crinoid; *Saccocoma tenellum* (Goldfuss), Solnhofen; maximum distance between the arms 40 mm; SM F11252. Photograph by K. Harvey, Cambridge University.

Starfish (asteroids)

Solnhofen starfish do not look much different from today's forms. The five arms merge into the central portion of the body which has the mouth on the underside. The underside of the arms is covered by enlarged plates out of which emerge tube feet. As both starfish and brittle stars normally fall apart during the fossilization process, the articulated specimens from the plattenkalk make a substantial contribution to our understanding of the evolution of these groups. The Solnhofen genera are relatively large, with diameters of up to 15 cm. However, all are rare and the figured *Lithaster* (fig. 7.52) is particularly uncommon.
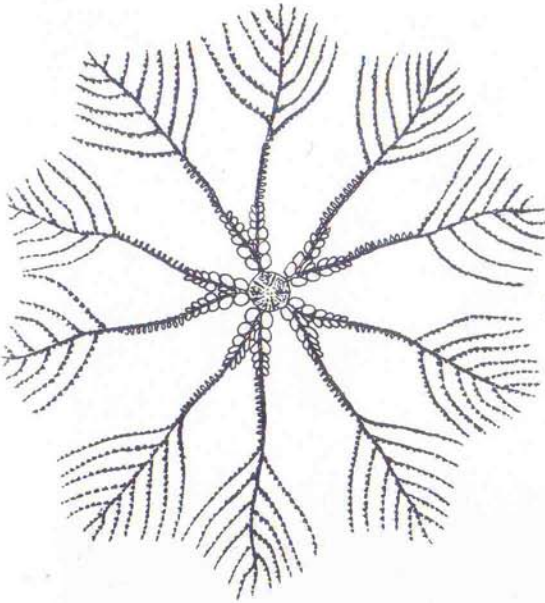
Fig. 7.50   Drawing of *Saccocoma*.

Brittle stars (ophiuroids)

Ophiuroids are typically smaller and more fragile in appearance than the asteroids, with the body disc distinctly demarcated from the long sinuous arms. The arms are strengthened by a series of fused ambulacral plates which resemble vertebrae and permit great mobility of the arms. Ophiuroids are mainly suspension feeders.

Geocoma (fig. 7.53) is very abundant in certain beds of the Zandt quarries. The body disc is small in proportion to the length of the arms, and the overall diameter is around 6 cm. *Ophiopsammus* (fig. 7.54) is larger than *Geocoma* with the body disc relatively larger in comparison to arm length. Characteristic features include a granulate pattern on the body disc, which is also present on the underside of the arms, a ridge over the upper arm plates and the presence of small arm spines. *Ophiopsammus* may be quite common in some parts of the Kelheim–Weltenburg region.

Sea-urchins (echinoids)

Echinoids have a globular test covered by spines. They are like starfish if one imagines the arms or ambulacra curled back away from the mouth and joined at the top of the animal, and the ambulacra became interconnected by interambulacral plates. Both the ambulacra and interambulacra may have spines, although sometimes of different shapes. The spines articulate by ball and
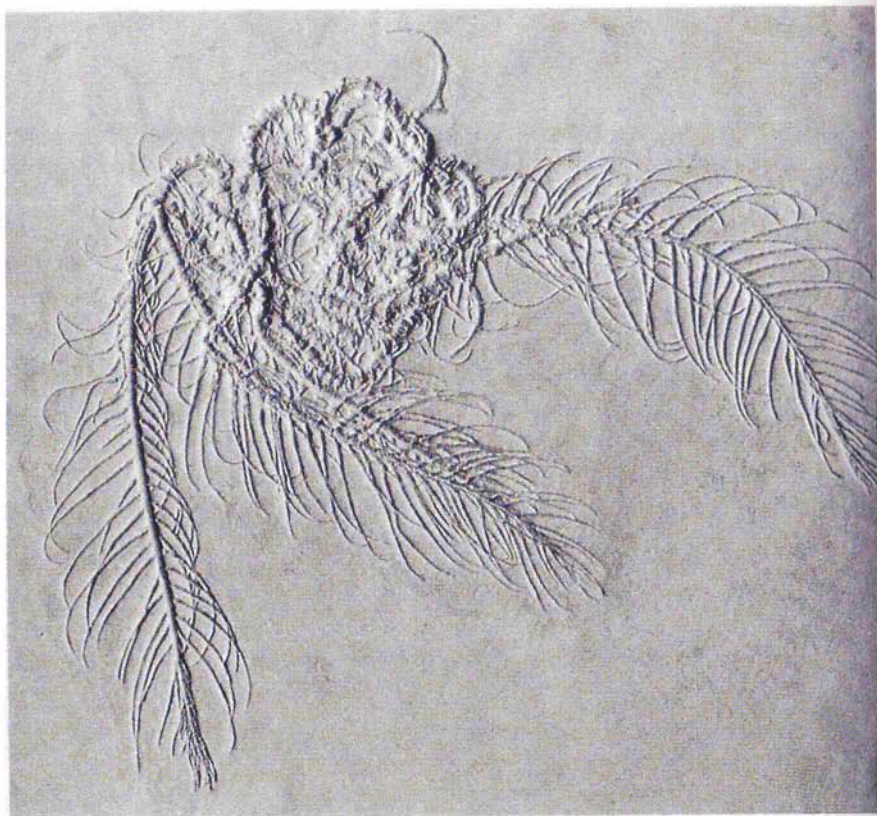
Fig. 7.51 Crinoid; *Pterocoma pennata* (Goldfuss), Zandt; maximum distance between the arms 100 mm; preparation, photograph and collection by Captain G. Brassel, Flensburg-Mürwik.

socket joints to rounded bosses on the underlying plates. Shortly after death the spines fall away and become separated from the animal. However, in the plattenkalk, echinoids are found with their spines still attached.

The general shape of the test distinguishes two types of echinoid. The regular echinoids, which in today's reefal environments are mainly surface grazers and predators, are equipped with a strongly toothed jaw on the underside of the body and an anus at the opposite side of the apex. *Tetragramma* (fig. 7.55), at around 5 cm in diameter, is an example of a fairly small regular echinoid. It has (and had, before it was squashed) a fairly flat test and a mosaic of broad plates around the anus. It kept predators at bay with a hedgehog-like arrangement of fairly large spines. Their attachment bosses are present in two rows on each ambulacrum whilst on each interambulacrum there are four rows in the centre flanked by two rows on each side. The spines are short, pointed and finely
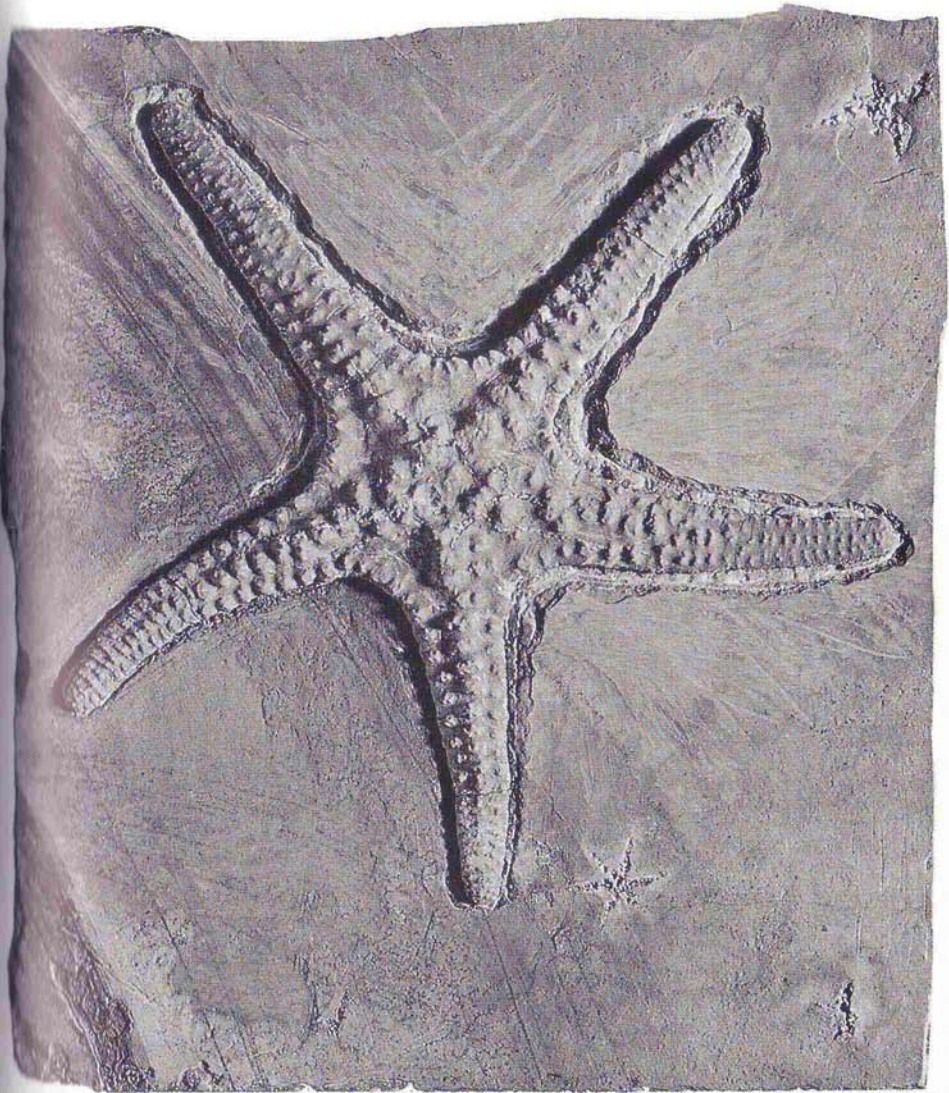
Fig. 7.52 Asteroid; *Lithaster jurassicus* (Zittel), Böhmfeld southeast of Eichstätt; maximum distance between the tips of the arms 140 mm; BSPHGM 1847 I 502. Photograph W. Suter, Naturhistorisches Museum, Basel.

striated. There are also several genera of echinoids from the cidaroid group in the Solnhofen Plattenkalk. These have very large club-shaped spines which may have been especially effective in deterring any would-be predator. These echinoids have a test of relatively few large plates with prominent bosses.
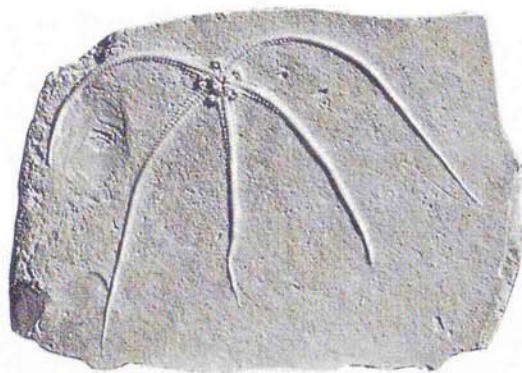
Fig. 7.53   Ophiuroid; *Geocoma carinata* Goldfuss, Zandt; maximum distance between arms 58 mm; BSPHGM AS I 555.

Fig. 7.54   Ophiuroid; *Ophiopsammus kelheimensis* (Boehm), Weltenburg bei Kelheim; BSPHGM 1965 XXIII 42.
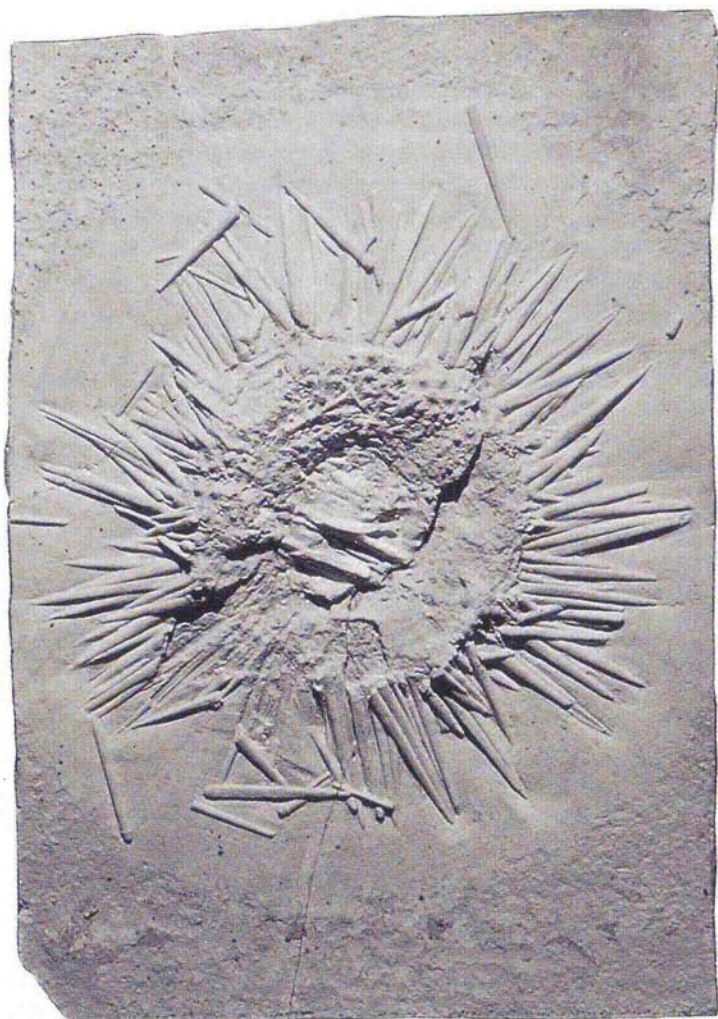
Fig. 7.55   Echinoid; *Tetragramma* sp., locality recorded as 'Solnhofen' but facies is more typical of Kelheim; diameter 50 mm; BSPHGM 1878 VI 8.

In the irregular echinoids the mouth remains on the underside of the animal (although it is often displaced from its central position), but the anus has migrated from the apex to a posterior position. In *Collyropsis* (unfigured) the test has the typical heart-shape in plan view. The pentameral symmetry of the beast has been disrupted by the imposition of a bilateral symmetry that reflects the greater mobility of the animal as it burrowed through the sediment, pursuing its life as a deposit feeder.

Sea-cucumbers (holothurians)

Holothurians are shaped like stretched-out echinoids, the mouth at one end, usually surrounded by tentacles, and the anus at the other. Moreover, calcareous plates are reduced to small microscopic ossicles, isolated from each other and embedded in the skin. On death the ossicles disperse, with the large number making them an important contribution to the sediment. The forms which live on the seafloor are protected by a leathery skin, whilst those which burrowed are more delicately built.

As expected, given their effectively soft-bodied nature, the fossil record of holothurian body fossils is extremely meagre. Thus the Solnhofen specimens, although of very poor quality, are of great palaeontological importance. *Protoholothuria* (unillustrated) serves as an example although it is extremely rare. It has a tube-shaped body, around 6 cm in length, with a coarsely granulate outer surface, and one end bearing five to six indistinct, shrivelled tentacles.

In some silicified portions of Solnhofen Plattenkalk, the calcite ossicles of holothurians may be replaced by silica and so may be dissolved out of the sediment by acid preparation in the laboratory. The small (0.1–0.3 mm) plates differ in shape and are assigned to various form-genera and form-species. It is recognized that these names are unlikely to correspond to original taxa of holothurians in as much as several ossicles of different sizes and shapes were present in the same body.

Vertebrates

FISH

The fish are by far the most numerous of the Solnhofen vertebrates, primarily because a few genera are found in great numbers at certain localities and stratigraphic levels. Most genera are, however, quite rare and only known from a few specimens. The Solnhofen fish may be conveniently classified into well-known living groups.

Shark-like cartilaginous fish (Chondrichthyes)

This includes three separate groups, the sharks and rays and the more distantly related ratfish. Instead of the heavy bony skeletons of their ancestors, their skeletons are made of the lighter and more flexible material, cartilage. A primitive characteristic present in both the Solnhofen and modern-day cartilaginous fish is a body covering of denticles or skin teeth. Each denticle contains an inner pulp cavity surrounded by dentine with an outer coating of enamel. The similarity between this arrangement and our own teeth is more than coincidental as they most probably evolved from denticles on the skin covering

the edges of the jaws. In cartilaginous fish the water necessary for respiration is drawn in through the mouth on the underside, as well as through a pair of circular structures known as spiracles (actually modified gill slits), and passed out through the remaining gill slits, which are usually located on the side of the animal.

Sharks (selachians)

Sharks move by sinuous curves of the tail, particularly of the upper flange, which provides the forward thrust. The body, being torpedo-shaped, is streamlined and the backbone may be weakly calcified for strength. The large lateral fins, or pectoral fins, act like the wings of an aeroplane providing an upwards thrust which counteracts the weight of the head and the tendency of the animal to nose-dive. As the overall body density is greater than the water, sharks must still keep moving in order to remain afloat. The continual swimming makes them either active hunters searching for and chasing prey, or else suspension feeders filtering the seawater. Sharks' teeth are usually sharply pointed but in some forms there may be flatter teeth adapted for crushing. The jaw is not attached to the brain case, but is supported behind a modified gill arch. Five types of sharks are recognized from the Solnhofen Plattenkalk.

The **Galeoidea** contains the majority of the living sharks, most of which are harmless enough, around a metre in length, and inhabiting areas of the world's oceans. Many are to be found in the North Sea, where they feed on fish. Amongst the Solnhofen assemblage *Palaeoscyllium* (fig. 7.56), has the typically long and narrow body of the galeoid sharks and prominent unpaired fins, two dorsal and one anal, without supporting spines. The paired fins are visible, although only in oblique orientation, and the tip of one of the pectoral fins protrudes slightly above the head. The vertebral column is very prominent, as the vertebrae are heavily calcified. In the fossil, the gill slits are no longer recognizable and the spiracle is known to be absent in this genus. The left eye appears slightly elevated from the surface, whilst the right one, which is only just visible, is pushed to the top of the skull. The teeth (not really visible in this photograph, but relatively frequently found detached from the body) have sharp cutting edges with one main point, or denticle, and sometimes smaller associated denticles.

Pseudorhina (fig. 7.57) is placed in the **Squaloidea**. This type of shark resembles a ray in its dorso-ventrally flattened body, well suited for gliding over the seafloor. Unlike a ray, the gill slits (accompanied by a large spiracle) open on the side of the animal and the mouth, with small rasping teeth, is situated at the front of the head. In addition, the pectoral fins are very large and clearly separated from the head, the pelvic fins being somewhat smaller. As in all squaloid sharks, there is no anal fin and although the spines supporting the dorsal fins do occur in related genera, such as *Protospinax* (unfigured), in *Pseudorhina* they are absent. The vertebrae are weakly ossified.
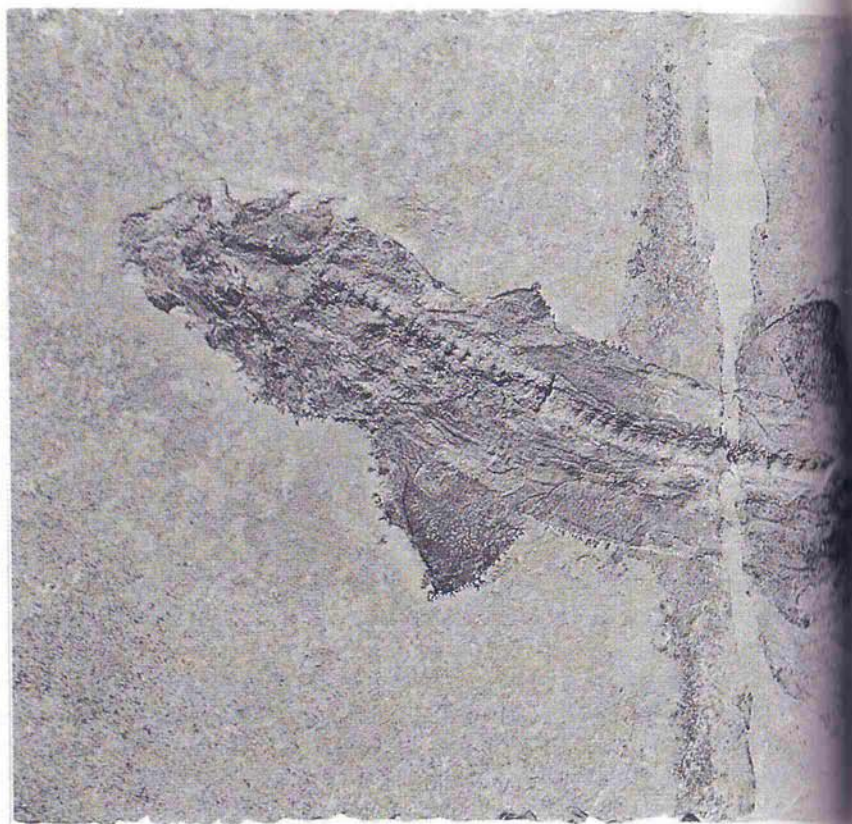
Fig. 7.56 Shark; *Palaeoscyllium formosum* Wagner, Solnhofen; length 313 mm; BSPHGM AS I 589.
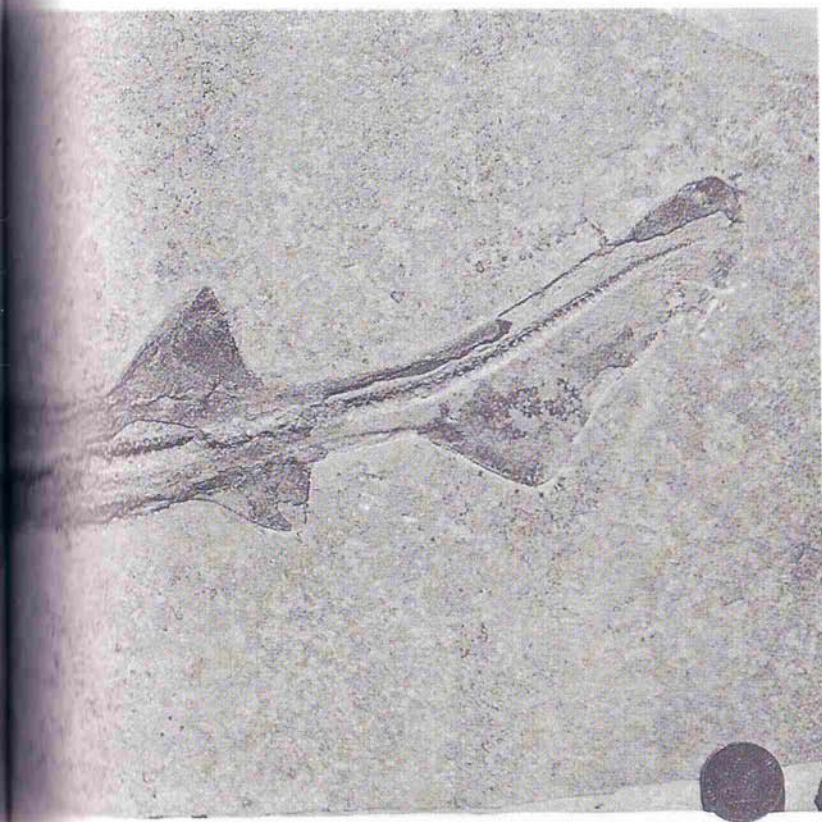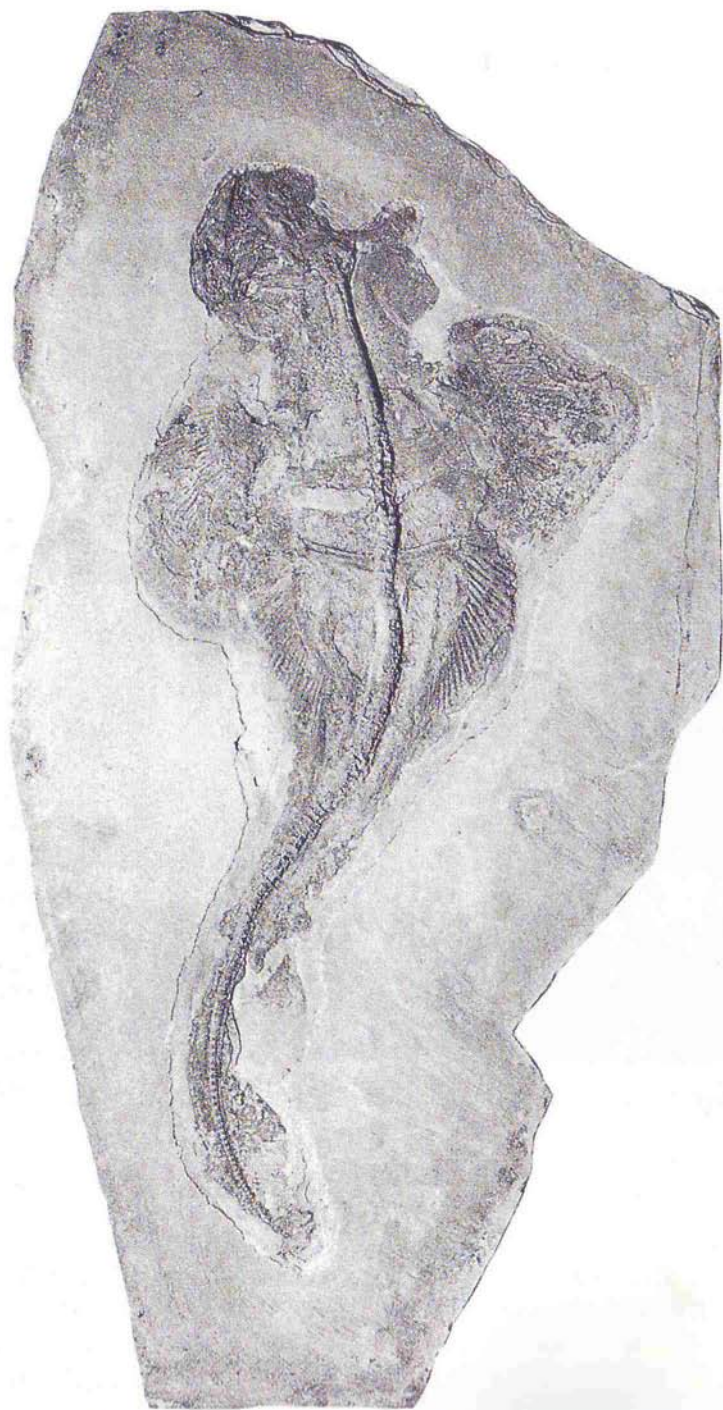
Rays (batoideans)

Rays have abandoned the life of continual motion needed by most sharks to keep them in mid-water. Instead they live on the bottom, camouflaged or slightly covered by the sediment. The tail is now no longer of prime importance in swimming and the muscles have diminished leaving a whip-like organ useful only in navigation. The ray moves by passing ripples along the pectoral fins, which are very large and fused to the head. The mouth is on the underside of the animal as rays feed on molluscs and crustaceans from the seafloor which they chew with a battery of small teeth, united in thick rows, or in a chewing palate. A current of water must be supplied to the gills, but to avoid also inhaling sediment, water is drawn in through the spiracles on the top of the head and then ejected through the gill slits which are always on the lower side of the body. Fig. 7.58 shows *Aellopos*, probably a relation of the modern 'guitar fishes', such as *Rhinobatus*. It does not show the extreme flatness of some of the rays and is still torpedo-shaped, like the sharks, although it is widened laterally by its pectoral and pelvic fins. However, the pectoral fins pass into the side of the head and the mouth and gills are on the underside making *Aellopos* a true ray. Dorsal and tail fins are also well developed, the dorsal fins each supported by a spine. This example is a male and is recognized by the supporting struts of the pectoral fins.

Chimaeriformes, ratfish (holocephalians)

This third group of cartilaginous fish is only distantly related to the sharks and the rays. The upper jaw is fused to the skull for extra strength, and hence gives the name to the group, Holocephali. The vertebrae are not additionally calcified. The few teeth are strong and flat rather than pointed and are used for crushing shellfish. Unlike the sharks and rays the gills are protected by a lobe of skin, which is not dissimilar in construction to that of the bony fish. The first dorsal fin is supported by a strong spine. *Ischyodus* (fig. 7.59) is a typical Chimaera, one of the two types of Solnhofen ratfish. The head is particularly large and slants forward, whilst the body tapers backwards producing a streamlined shape. The spine of the first dorsal fin is clearly visible behind the head whilst the second dorsal fin is elongate and of small size. Both paired pectoral and pelvic fins are large.

Bony fish (Osteichthyes)

Ray-finned fish (actinopterygians)

Of the bony fish, the main type found in the Solnhofen Plattenkalk are the ray-finned fish, so called because the fins are supported by strong bony rays or

Fig. 7.57 Shark; *Pseudorhina alifera* (Münster), Eichstätt; total length 463 mm; BSPHGM AS VII 4.
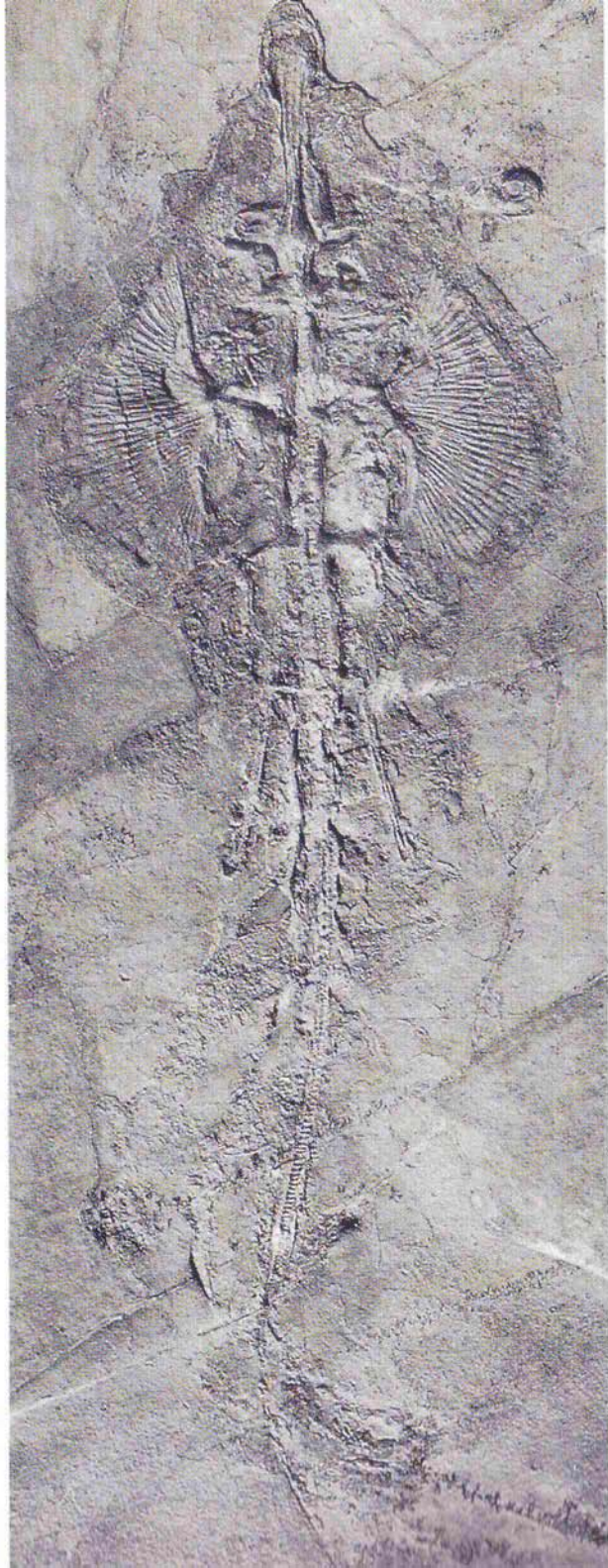
spines. There are three groups, two of which, the **Chondrostei** and the **Holostei**, may be intermediate in the evolutionary road to the modern bony fish, the **Teleostei**.

Cartilaginous ganoid fish, or **chondrosteans**, may be considered the most primitive. They are covered by a restrictive coat of thick, enamel-covered scales (ganoid scales). The scales are firmly held together in rigid circles around the body, but these may articulate between one another. This allows the body to bend side to side in snake-like movements, but not to change in shape. The vertebrae remain unossified. The tail and pectoral fins are still required to produce an upward thrust for the heavy body (even though the fish may possess a swim-bladder). The tail shape remains asymmetrical with the upper flap supported by the vertebral column and the lower flap fleshy and not covered with scales. A living relative of the chondrosteans may be the caviar-producing sturgeon. From the Solnhofen Plattenkalk only one species of the genus, *Coccolepis* (unfigured), is recorded.

Bony ganoid fish, or **holosteans**, make up most of the Solnhofen fish. A bony inner skeleton takes over the function of movement regulation making the strong and heavy scale coating of lesser importance, especially for those forms which are rounder in cross-section and less susceptible to distortion. Scales are intermediate between rhomboid ganoid scales and overlapping round cycloid scales. The tail is generally smaller than in the chondrosteans and in some forms may be almost symmetrical. A swim-bladder enables the fish to be neutrally buoyant. The mouth region has become shortened and the upper jaw more manoeuvrable.

The specimen of *Lepidotes* (fig. 7.60) is the most noteworthy of the Solnhofen holosteans because of its extremely large size, which may reach 2 m in length. However, entire specimens of *Lepidotes* are generally very rare. The thick, enamel-covered scales are very prominent and are more often found disarticulated from the skeleton, as are the hemispherical teeth.

Gyronchus (fig. 7.61), belongs to a different group within the holosteans, and resembles the modern parrot fish. The body is very thin and disc-shaped, supported internally by a delicate network of bones, and the front part is covered externally by large scales. The fish manoeuvred by the dorsal, ventral and symmetrical caudal fin as well as the relatively small paired fins, enabling *Gyronchus* to weave between coral branches. *Gyronchus*, as well as its larger relative *Gyrodus*, has small round teeth (fig. 7.62), which in the parrot fish are adapted for chewing coral.

Fig. 7.58   Ray; *Aellopos bugesiacus* (Thiollière), Langenaltheim; width of pectoral fins 620 mm, BSPHGM AS I 506. Copyright of that collection. Photograph M. Dressler.

Fig. 7.59 Ratfish; *Ischyodus quenstedti* Wagner, Eichstätt; length 1550 mm; BSPHGM 1954 I 366. Copyright of that collection. Photograph M. Dressler.
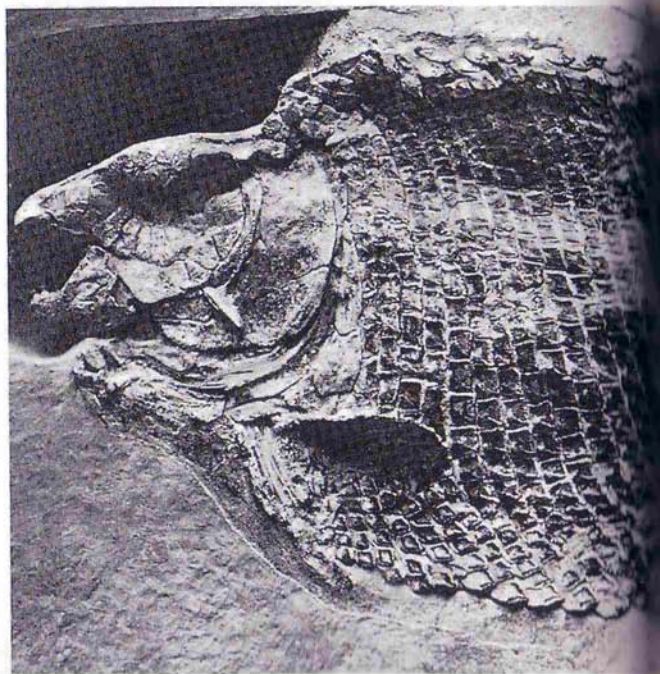
Fig. 7.60 Semionotiform, holostean fish; *Lepidotes maximus* Wagner, Langenaltheim; length 2050 mm; NMSF P 2886. Copyright of that museum.
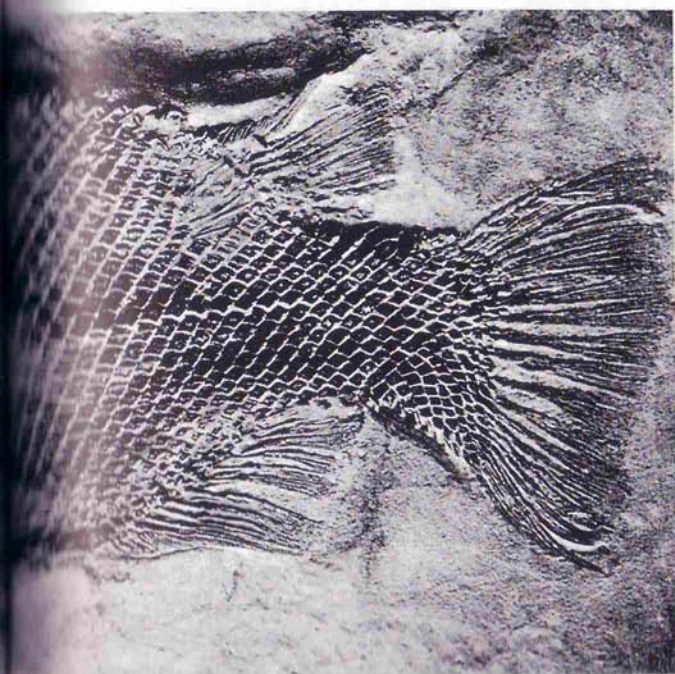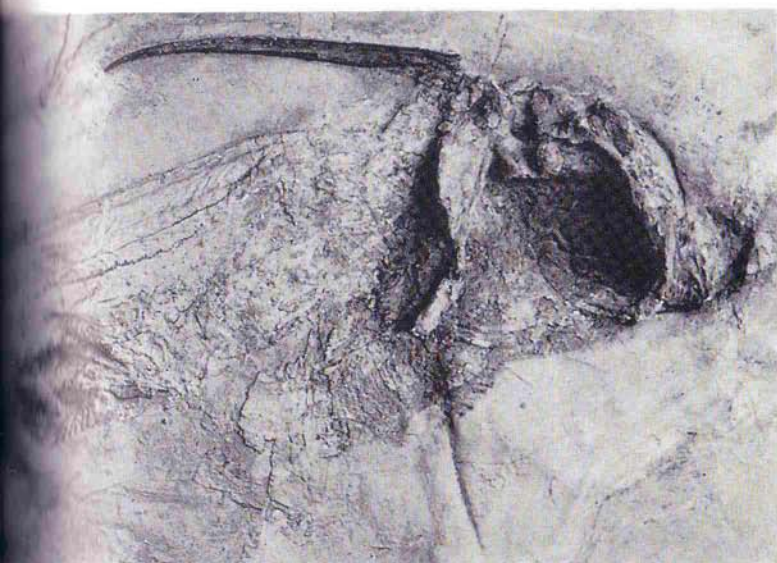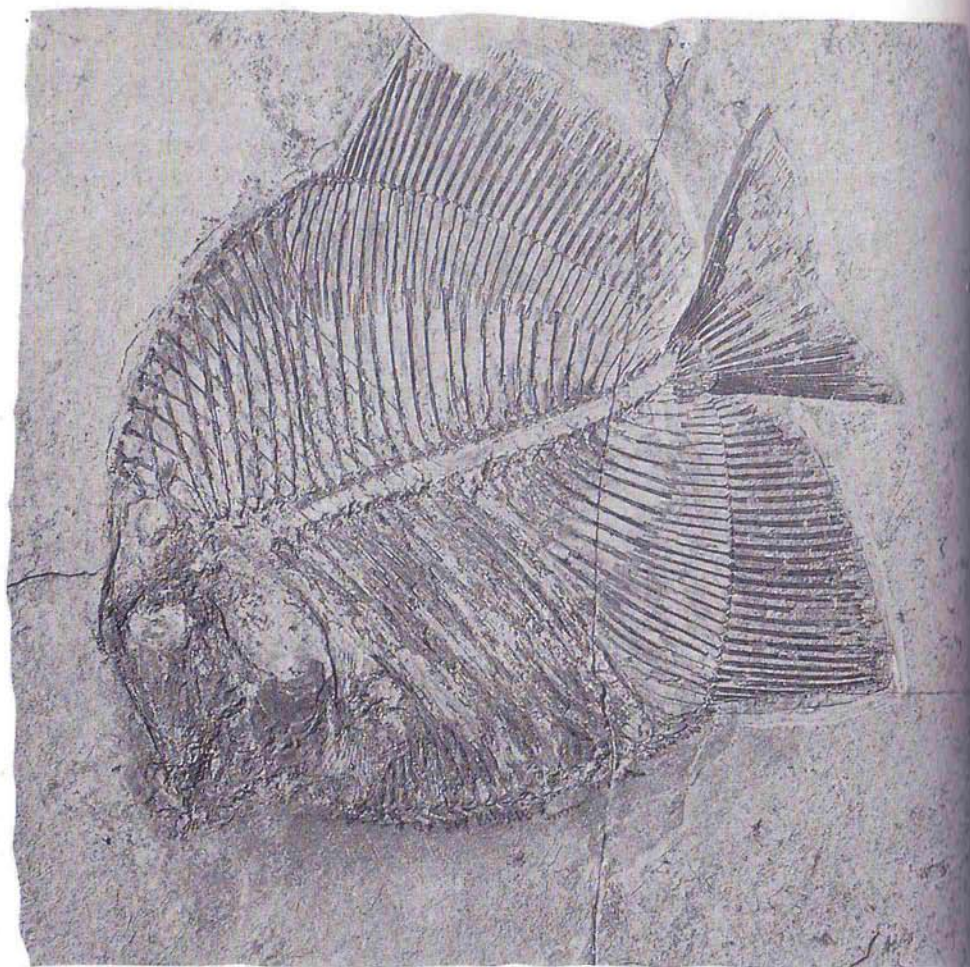
Fig. 7.61 Pycnodontiform, holostean fish; *Gyronchus macropterus* (Wagner), Blumenberg bei Eichstätt; total length 162 mm; BSPHGM 1939 I 19.

Caturus (fig. 7.63), with a streamlined body and almost symmetrical deeply forked tail, must have been an agile and fast-moving swimmer. It too possesses a thick covering of scales, which conceals the vertebral column. Juveniles (such as the figured example) still had unossified vertebrae which do not preserve well. On the ventral side the intestinal contents are preserved in phosphate. The related *Urocles* (unfigured) has a body shape which indicates that it too was a good swimmer and an active predator. It is easily recognizable from its brush-like tail. The remains of smaller fish on which it preyed have been found in the gut of some specimens. *Urocles* specimens are peculiar in that they have never been found on the bedding planes, but occur inside flinz units on minor planes
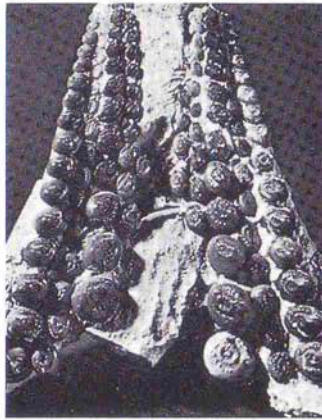
Fig. 7.62 Teeth of *Gyrodus circularis* Agassiz, Solnhofen?, approximately natural size; BSPHGM 1972 XX 137.

of weakness. From another related family comes **Histionotus** (fig. 7.64), which has very large and distinctly shaped dorsal and caudal fins which could have enabled precise navigation amongst the reefs.

A very different shape is demonstrated by the elongate, pike-like **Aspidor-hynchus** (fig. 7.65) and related **Belonostomus** (fig. 7.66). The scales are large on the flanks but small on the underside and back. When the fish died and started to decay the scales tended to stay together and become detached from the underlying tissue as a scale envelope (see p. 91). The best-preserved specimens are of moderate size and have been obtained from Zandt and Kelheim.

Lastly **Pholidophorus** (unfigured) is a holostean which possesses some of the traits of the modern bony fish, the Teleostei. In outline *Pholidophorus* looks rather like the modern herring and it may have had a similar life style. The body is spindle-shaped and the tail symmetrical. The skull shows the 'advanced characteristics' of a movable upper jaw, and in a related genus the lower jaw protrudes over the upper. The vertebrae are fully ossified. The armour of scales is lighter, the scales being thinner.

Modern bony fish, or **teleosts**, have a skeleton which is completely ossified and supports the body. The scales, which are no longer needed for support, are small and round and constitute the body covering. The body is a simple spindle shape with a deeply forked symmetrical tail. The upper jaw is movable. All of the Solnhofen fish belong to the same group as the modern herring although some reached a size of around a metre. The aesthetically pleasing **Pachythris-sops** (fig. 7.67) is a typical example. The sprat-like fish assigned to the genus **Leptolepides** (fig. 6.4, pp. 94–5) are undoubted teleosteans but are probably juveniles belonging to a variety of separate species. These small, superficially similar, fish occurred in swarms such as are preserved in the so-called Solnhofen "*Fischflinz*" (see p. 92).
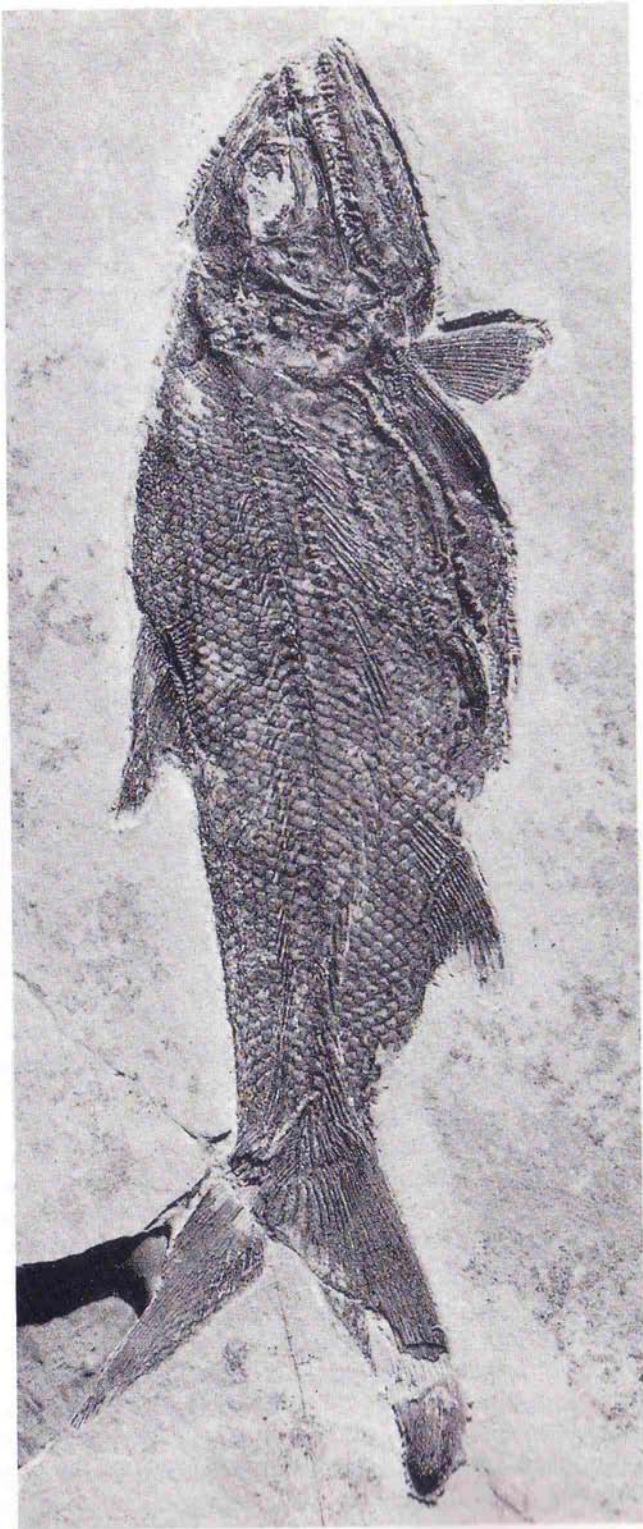
Lobe-finned fish (crossopterygians)

These are also bony fish but only distantly related to the Actinopterygii. The lobe-finned fish are very important in vertebrate evolutionary history as one group of these is thought to have given rise to the amphibians by the development of limbs and an internal nostril. The **coelacanths** lack an internal nostril, and have modified the primitive lung into an air-filled swim-bladder with ossified walls. In the Solnhofen coelacanths we can see the characteristically peculiar fin structure with the stout base and brush-like end, which, in Palaeozoic forms, evolved into the limbs of modern land animals. *Coccoderma* (fig. 7.68) is a small coelacanth with a narrow body and pelvic fins in an anterior position near to the pectoral fins. It has a prominent scale covering and the vertebral column is unossified. The weakly ossified swim-bladder is seen near the front of the body, visibly outlined by a brown stain.

REPTILES

The Solnhofen Plattenkalk has yielded a varied selection of reptiles whose habitats were either marine or terrestrial. The primary classification of the reptiles is based on the number and position of the skull openings which allow for a bulging of muscles when they are relaxed (see fig. 7.69).

Turtles (chelonians)

The turtles are **anapsid reptiles** (fig. 7.69a). In this group the only skull openings are those of the eyes, nostrils and brain stem. The most obvious feature of the turtles is their body armour, consisting of upper and lower shells. The upper shell is made of an intergrowth of ribs, backbone plates and other marginal plates, and the lower shell of the lower rib cage and parts of the shoulder girdle. In modern turtles the shell is overgrown by a horny substance, which is not preserved in these fossils. In some turtles, including some Solnhofen genera, the armour is lightened by leaving 'windows' between the plates presumably to facilitate swimming. However, the Solnhofen turtles cannot have been true open-sea swimmers (as is the example in fig. 7.70) because instead of fins they had stumpy toed limbs which were evidently ill-adapted to swimming. They probably lived partly in freshwater and partly along the sea coast. All specimens found so far are, at half a metre in length, small in comparison to today's turtles and may be juveniles. Of the four easily recognizable genera from the Solnhofen Plattenkalk *Eurysternum* is figured (figs. 7.71 & 7.72). This genus is characterized by a shallow shell with narrow,

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Fig. 7.63 Amiiform, holostean fish; *Caturus furcatus* Agassiz, Schernfeld bei Eichstätt; total length 165 mm; BSPHGM 1964 XXIII 159.
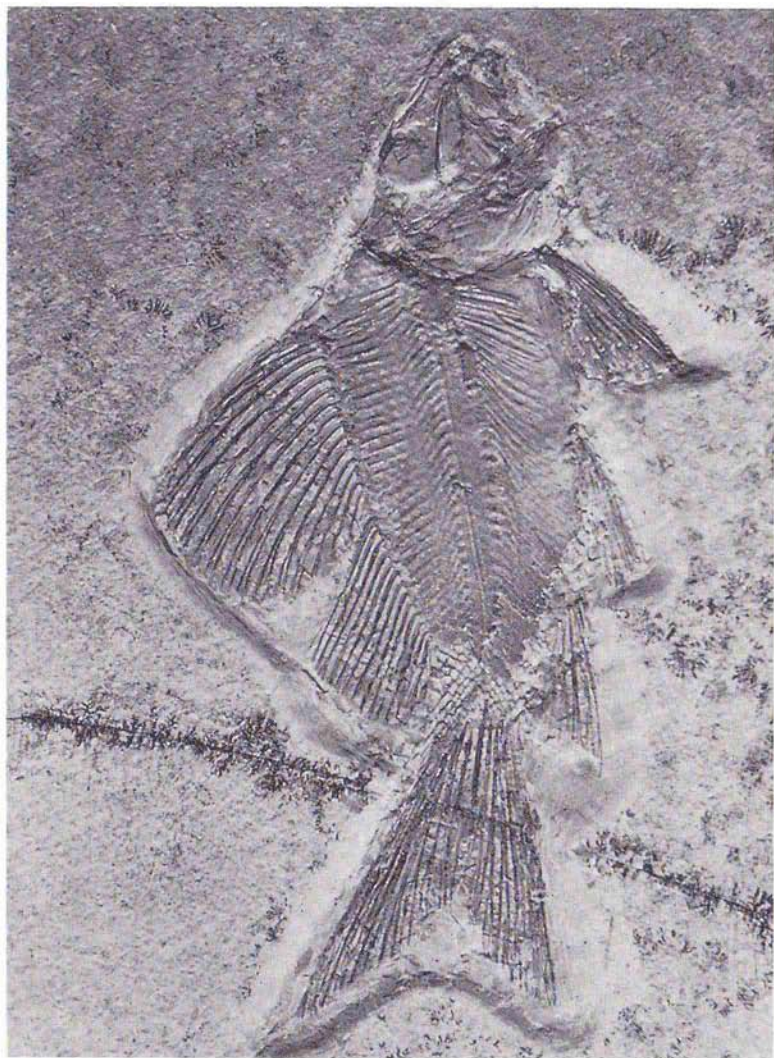
Fig. 7.64 Amiiform, holostean fish; *Propterus elongatus* Wagner, Blumenberg bei Eichstätt; total length 138 mm; Museum Bergér, Harthof bei Eichstätt.
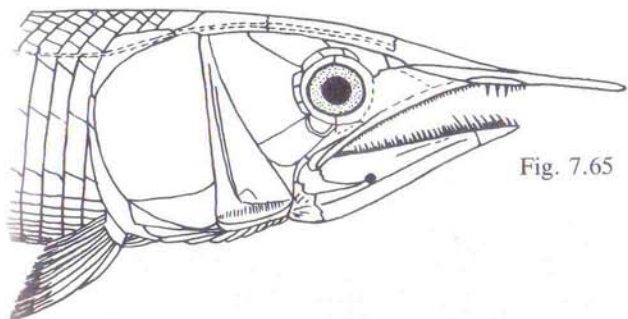
Fig. 7.65 Drawing of *Aspidorhynchus*.

Fig. 7.66 Aspidorhynchiform, holostean fish; *Belonostomus muensteri* Agassiz, Zandt; length 345 mm; BSPHGM 1957 I 339.
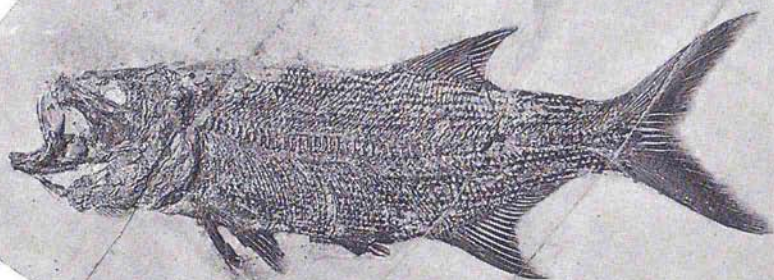
Fig. 7.67   Teleost fish; *Pachythrissops propterus* (Wagner), Painten bei Kelheim; total length 385 mm; BSPHGM 1964 XIII 154.
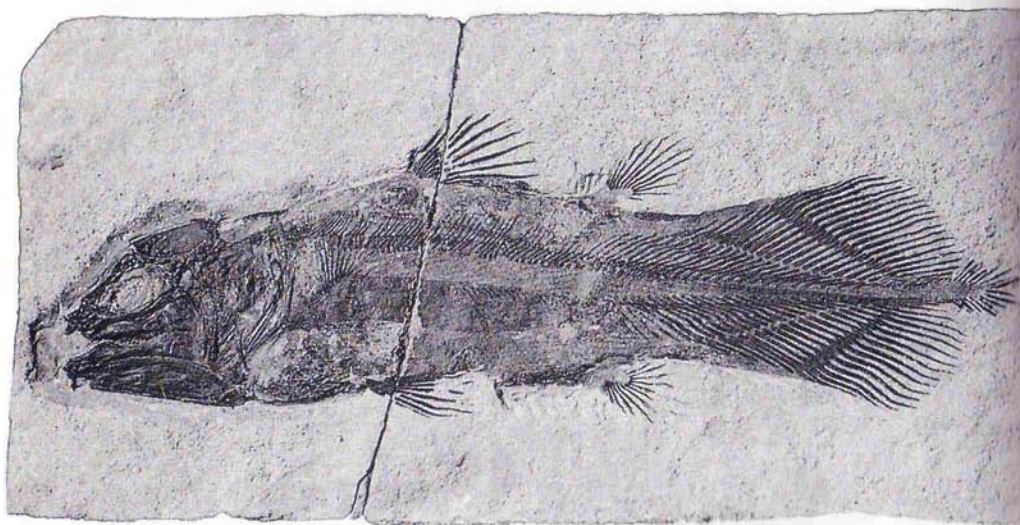
Fig. 7.68   Crossopterygian fish; *Coccoderma nudum* Reis, Kelheim; total length 188 mm; BSPHGM 1887 VI 501.
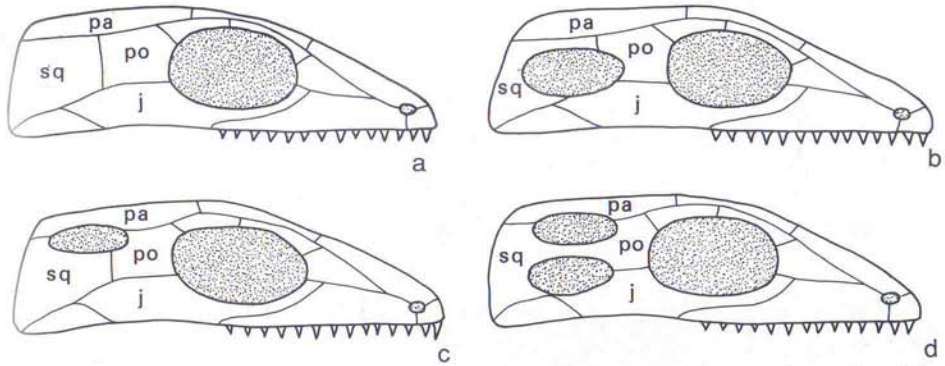
Fig. 7.69 Side views of reptilian skulls to show various types of temporal opening. (a) No opening: 'anapsid' condition. (b) A lower opening with postorbital and squamosal meeting above: 'synapsid' condition. (c) An upper opening with postorbital and squamosal meeting below: 'parapsid' condition. (d) Both openings present: 'diapsid' condition. Abbreviations: j, jugal; pa, parietal; po, postorbital; sq, squamosal. From Romer (1962).
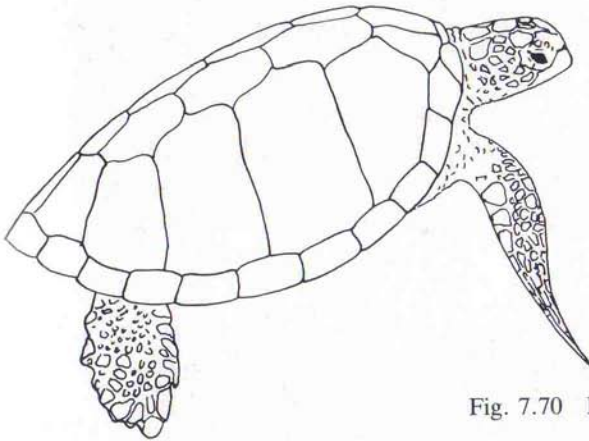
Fig. 7.70 Drawing of modern sea turtle.

marginal 'windows'. The lower shell too shows one central and two lateral openings.

Ichthyosaurs

Ichthyosaurs, as most swimming reptiles (apart from the turtles), are parapsid. They have one additional skull opening, high on the head and bordered on the lower side by a bar of bone (fig. 7.69c). They are well adapted for swimming, with a streamlined shape and limbs converted to fins (fig. 7.73). Their long
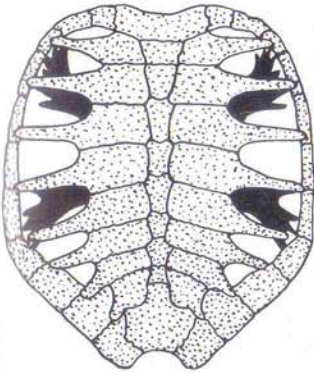
Fig. 7.72   Reconstruction of *Eurysternum* carapace.
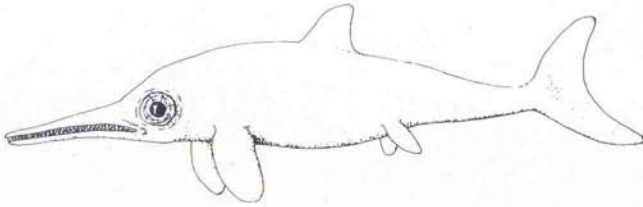
Fig. 7.73   Reconstruction of the ichthyosaur animal.

snout, numerous teeth and large eyes all suggest they were predators of the open sea. The vertebral column dips sharply downwards in the tail region. This is known not to be a post-mortem feature, because some specimens from the Lias shales of Holzmaden in southern Germany are preserved with an outline of skin around the downwardly deflected vertebral column. The paddle-like paired fins probably functioned as stabilizers rather than rudders. A few specimens from Holzmaden are preserved with young inside which, like their ecological descendant, the whale, would be born alive and tail-first into the water. Although ichthyosaurs are common in the quarries of Holzmaden, such large creatures of the open sea did not often find their way into the Solnhofen lagoons. Fig. 7.74 shows one of only two genera known from the Solnhofen Plattenkalk, *Macropterygius*. It is a partially disintegrated corpse, the tail and posterior fins having already fallen away and been lost.

Plesiosaurs

Plesiosaurs were also large, swimming reptiles well adapted to deeper waters. They have two giant pairs of paddles on a rather plump body. To make room

Fig. 7.71   Turtle; *Eurysternum wagleri* Meyer, Kelheim; skull length 66 mm; BSPHGM AS I 818.

Fig. 7.74 Ichthyosaur; *Macropterygius posthumus* (Wagner), juvenile, Solnhofen; maximum diameter of eye socket 83 mm; BSPHGM 1954 I 508.

for massive paddle muscles, as well as a protection against water pressure, the shoulder girdle and pelvic elements are widened to enormous bony plates. One of the two types of plesiosaur is known from the Solnhofen Plattenkalk. It probably lived in the open sea and made forays into the lagoon, on one occasion leaving behind a tooth. The large size of the tooth, some 23.5 cm in length, suggests the entire animal was not less than 12 m long.

Lizards (lacertilians)

The lizards and snakes together with the lizard-like rhynchocephalians all belong to the Lepidosauria. The lepidosaurs, crocodiles and dinosaurs are all **diapsid** reptiles, characterized by two additional pairs of skull openings (fig. 7.69d). In the lizards, the lower opening has lost its lower margin and is therefore open below, unlike the rhynchocephalians, which retain a bar of bone in this position. The skulls can be compared in fig. 7.75 but unfortunately not all specimens are well enough preserved to permit this discrimination. Only a very few Solnhofen lizards are known and are assigned here to five genera. *Eichstaettisaurus* is figured (fig. 7.76), but it may not warrant distinction at a generic level from *Ardeosaurus* which has two fewer thoracic vertebrae. On *Ardeosaurus* the narrow, upper skull opening is clearly visible, the vertebrae
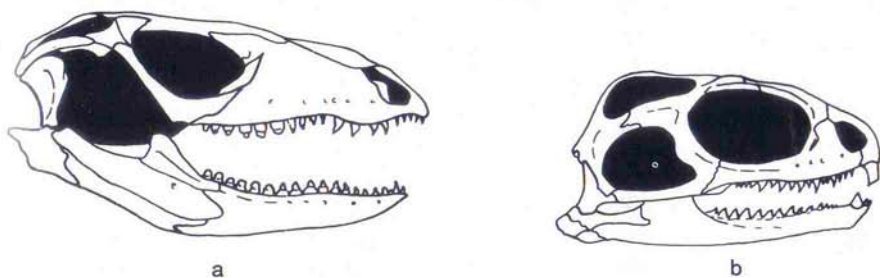
Fig. 7.75   Skulls of (a) lizard and (b) rhynchocephalian.

are large and strong, and the neck squat. These rather stout lizards may be relatives of the modern skinks. Their habitat can hardly have lain in the coastal regions because specimens are found so rarely in the lagoon. Even the few rhynchocephalians are more common than these true lizards.

Fig. 7.76   Lizard; *Eichstaettisaurus schroederi* (Broili), Wintershof bei Eichstätt; skull length 19 mm; BSPHGM 1937 I 1.

Rhynchocephalians

The beaked lizards from the Solnhofen Plattenkalk are of similar small size to the true lizards and the nearest living relative was thought to be *Sphenodon*, from New Zealand (fig. 7.77). Rhynchocephalia means 'beaked head', which is a reference to the shape of the snout. Apart from a few problematic forms the species can be accommodated in two genera; **Kallimodon** (fig. 7.78) has a longer and narrower skull than its relative **Homeosaurus** (unfigured), both having elongate skull openings. A small chamber is often preserved in the apex of the skull. *Kallimodon* was about a quarter the size of *Sphenodon*, with shorter and stouter appendages.

The swimming lizards, such as **Pleurosaurus** (fig. 7.79) and the smaller **Acrosaurus** (possibly a juvenile of *Pleurosaurus*), are probably also members of the Rhynchocephalia. Since they all have a beaked skull, elongate body and short legs, the lack of the lower skull opening is probably secondary. The little legs would probably have functioned on land but were more often used in the water as stabilizers. With its snake-like form and laterally compressed tail *Pleurosaurus* was probably a highly efficient swimmer in the manner of an eel. The nasal openings at the top of the head are fairly far back so that the animal needed only to bring its head to just above the water surface in order to
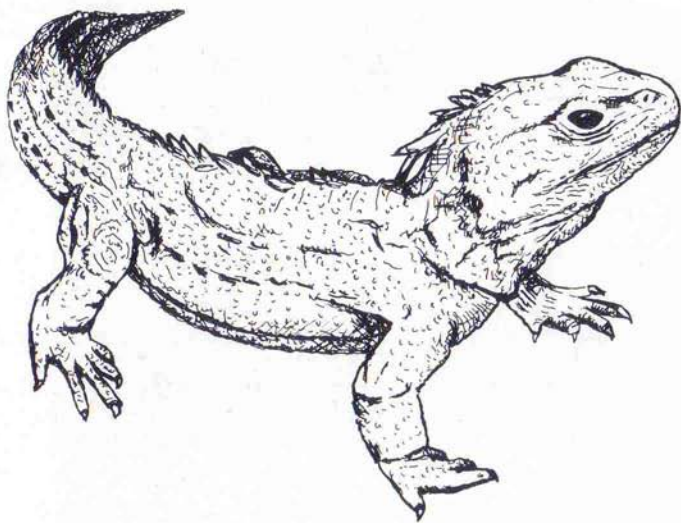
Fig. 7.77 Drawing of purported rhynchocephalian from New Zealand *Sphenodon*; approx. length 600 mm.

Fig. 7.78 Rhynchocephalian; *Kallimodon pulchellus* (Zittel), Painten bei Kelheim; length 175 mm; BSPHGM 1887 VI 2.
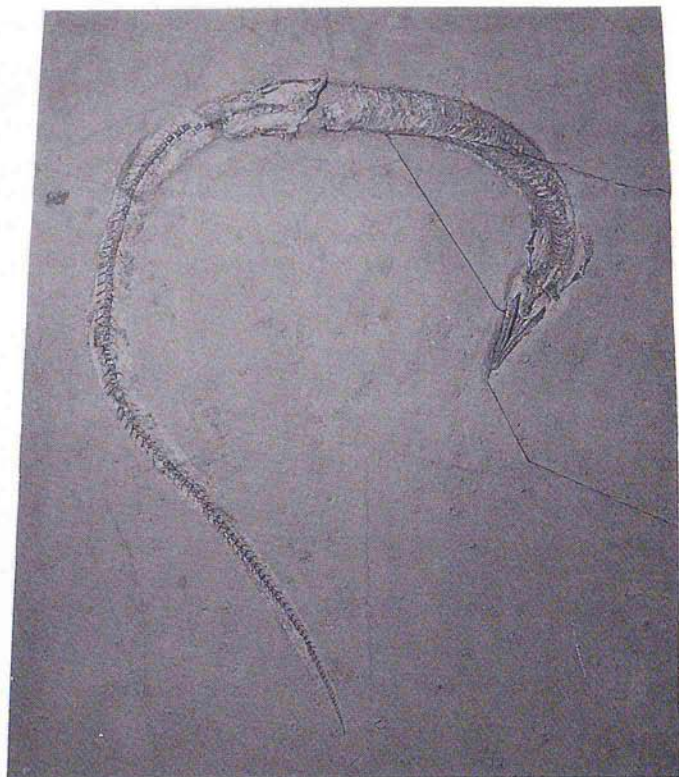
Fig. 7.79 Rhynchocephalian; *Pleurosaurus goldfussi* Meyer, Sappenfeld bei Eich-stätt; length 1520 mm; BSPHGM 1925 I 18.

breathe. It also bore six-sided scales. *Pleurosaurus* is found most frequently where there is an accumulation of driftwood which suggests that it lived in a stream and its dead body was washed into the lagoon.

Crocodiles

Crocodiles are also diapsid reptiles. All the Solnhofen specimens have an inner nasal opening which is not shifted as far back as it is in the modern crocodiles. There are three types of Solnhofen crocodile. The first, exemplified by **Alligatorellus** (fig. 7.80), is a small crocodile by modern standards at only 50 cm long, and much of the body is covered by an armour of bony plates. The long limbs enabled the animal to hunt on land as well as in the water. As is the case for all land animals, the Solnhofen Plattenkalk has yielded few specimens and they have all come from the Eichstätt and Kelheim regions.

The second type are coastal crocodiles, but these are extremely rare. A reconstructed specimen of **Steneosaurus**, some 4 m in length, is on display in
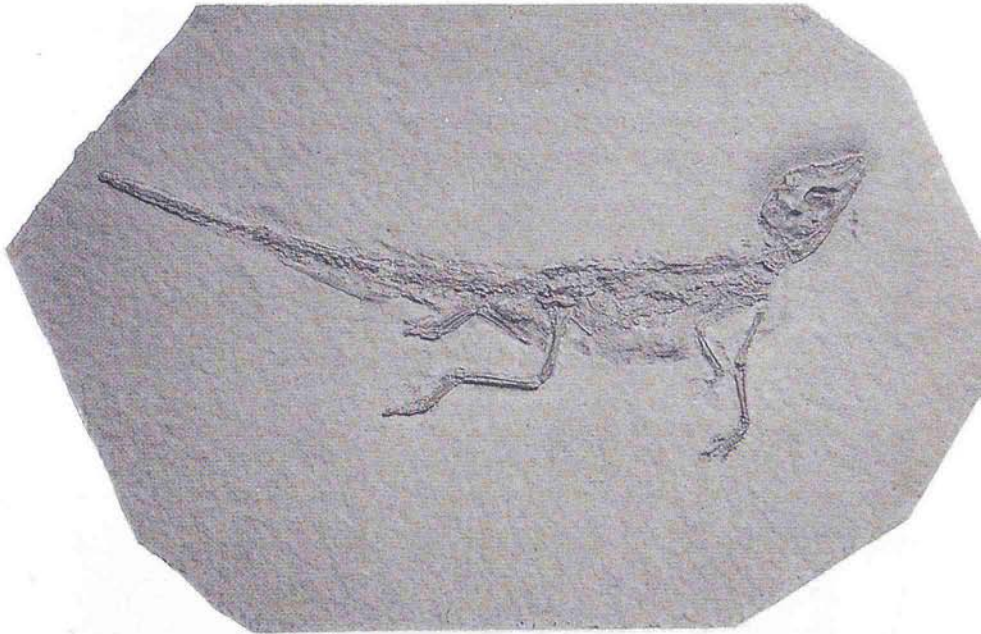
Fig. 7.80 Crocodile; *Alligatorellus beaumonti* Gervais, Eichstätt; length 305 mm; BSPHGM 1937 I 26.

the Jura-Museum in Eichstätt. Its long skull suggests that it preyed on fish. It has paddle-like limbs, one of which has a membrane still preserved between the toes. The back and underside were covered by protective bony plates and the flanks probably bore a scaly skin. The single specimen of **Aeolodon** (now missing), which was described from the Daiting plattenkalk, may also belong to this genus.

The last group of crocodiles is of such different construction that many workers would place it in a separate suborder. *Geosaurus* is a small elegant form of around 2 m in length. The limbs are modified to fins and the bony armour plating has been abandoned to facilitate movement through the water. A vertical tail fin and a fine ridge along the underneath and back of the animal were also new developments. The skull is lightly built and in the narrow jaws are set small teeth of equal size. Similar sets of teeth in other groups are usually a hallmark of life spent hunting in the open sea.

'Dinosaurs'

The term dinosaur was invented to include all the giant land reptiles and is generally regarded as an unnatural grouping. There are two groups, the Saurischia and the Ornithischia, which differ in the construction of the pelvis.

Fig. 7.81 Dinosaur; *Compsognathus longipes* Wagner, Jachenhausen bei Kelheim; width of picture *c*. 315 mm; BSPHGM AS I 563.

Not all the dinosaurs were gigantic in size. **Compsognathus** (figs 7.81, 7.82 & 7.83), which is the only dinosaur found in the Solnhofen Plattenkalk and represented by only this one specimen, is scarcely bigger than a chicken. *Compsognathus* is a coelurosaurian dinosaur, which is itself a subgroup of the Theropoda, and thus a member of the Saurischia. In the light and robust skull
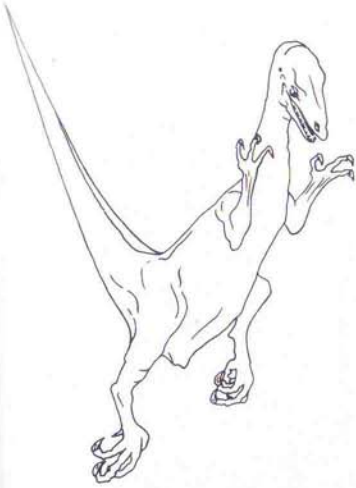
Fig. 7.82   Reconstruction of *Compsognathus*.
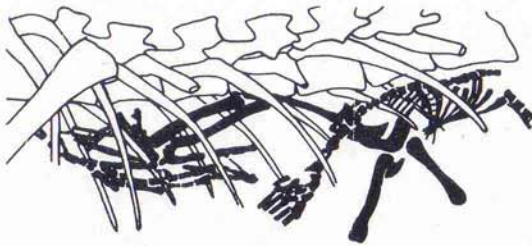
Fig. 7.83   Drawing of small lizard in the gut of *Compsognathus*.

there are two openings behind the eye holes and another between the eye and the nostrils. *Compsognathus* has a long, forward-leaning body counterbalanced by a thick tail. The two, strong, long hind legs, used for running, terminate in five toes. The forelimbs are short with two-fingered hands well adapted to gripping prey. On a long narrow neck, a small pointed head could be swivelled in search of prey. The jaws have the pointed, slightly backwards curving teeth suited to holding and gorging food. In this specimen, a small skeleton is preserved in the stomach. This was first thought to be an embryo, but then recognized as a small ground lizard, evidently the diet of *Compsognathus* (Ostrom 1978). The supposed tracks of *Compsognathus* from the Solnhofen Plattenkalk have since been recognized as limulid traces.

Pterosaurs

There have been three groups of vertebrates which have at various times taken to active flight. In Late Jurassic times birds were at the very beginning of their development. Flying mammals, including the bats, did not evolve until Ter-
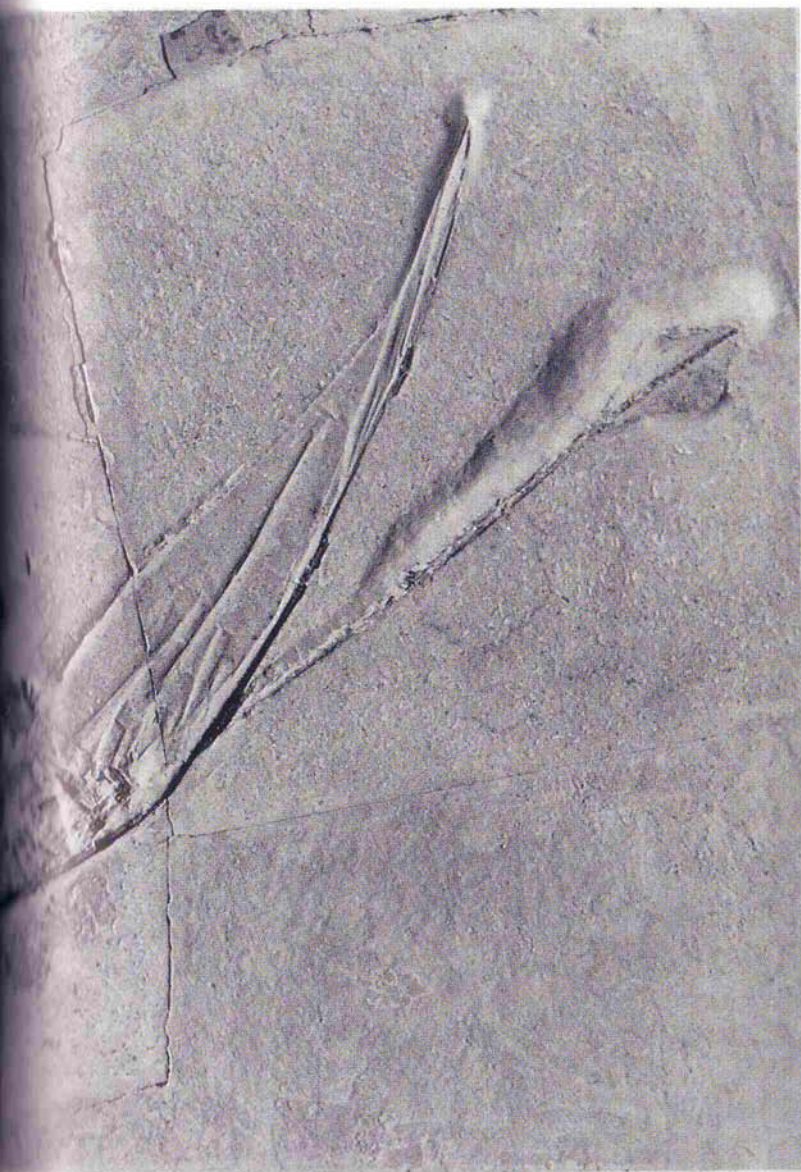
Fig. 7.84 Pterosaur; *Rhamphorhynchus muensteri* (Goldfuss), Eichstätt; length of skull 90 mm; Yale Peabody Museum, catalogue no. 1778; photograph lent by Professor J. H. Ostrom.

tiary times and it was the pterosaurs, winged relatives of the dinosaurs, who at this time reigned supreme. In Solnhofen times the pterosaurs, with wingspans averaging 1 m, were small by comparison with the giants of the Cretaceous who sometimes achieved wingspans of 15 m.

Pterosaurs have skeletons which are strongly, yet lightly built. On the forelimb, the fourth finger is very long and from its tip stretched the wing membrane which at its other end was attached to the body. The first three fingers articulated separately and were used for grasping, the fifth being lost in the course of development. In the extremely well-preserved Solnhofen specimens, hair-like structures may sometimes be seen on the wing membrane. In mammals a hairy covering is used to conserve internally generated heat, and if the 'hairs' of the pterosaurs had a similar role, it implies the pterosaurs, too, were warm-blooded.

Some pterosaurs may have been partly aquatic in their habits. This is adjudged both from the webbing between their hind toes and from the stomach contents, which include fish. In Jurassic genera, the teeth are small and numerous and would also be well adapted for a diet of insects. Of the two groups of pterosaurs, one includes *Rhamphorhynchus* (figs. 7.84, 7.85 & 7.86). This has a powerful, large skull with strong, forward-pointing teeth and a horny coating on its long snout. The most conspicuous feature is the long, rod-like tail with an upright rhombic-shaped vane at the end. The tail is strengthened by a process originating from two fused vertebrae. In *Pterodactylus* (fig. 7.87), the bones in the middle of the hand are considerably longer. The teeth are short and conical or else long and delicate. The very similar *Ctenochasma* (figs. 7.88 & 7.89) has an even finer array of small teeth, probably used for seizing small animals out of the water or for catching insects.
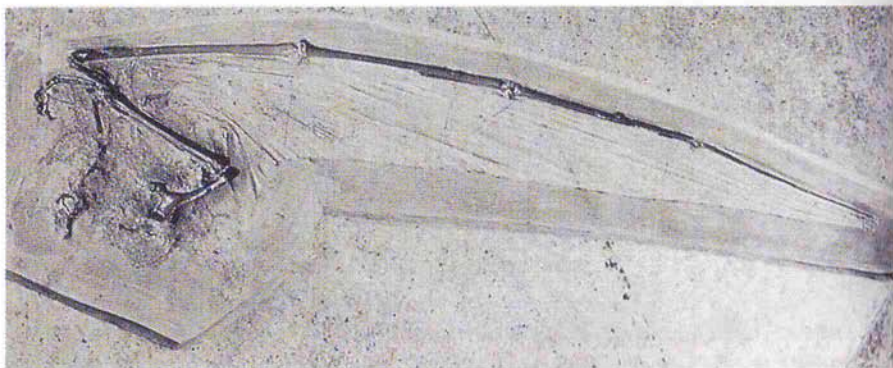
Fig. 7.85   Wing of *Rhamphorhynchus muensteri* (Goldfuss), Wintershof bei Eichstätt; length of wing bone 384 mm; BSPHGM AS I 771.
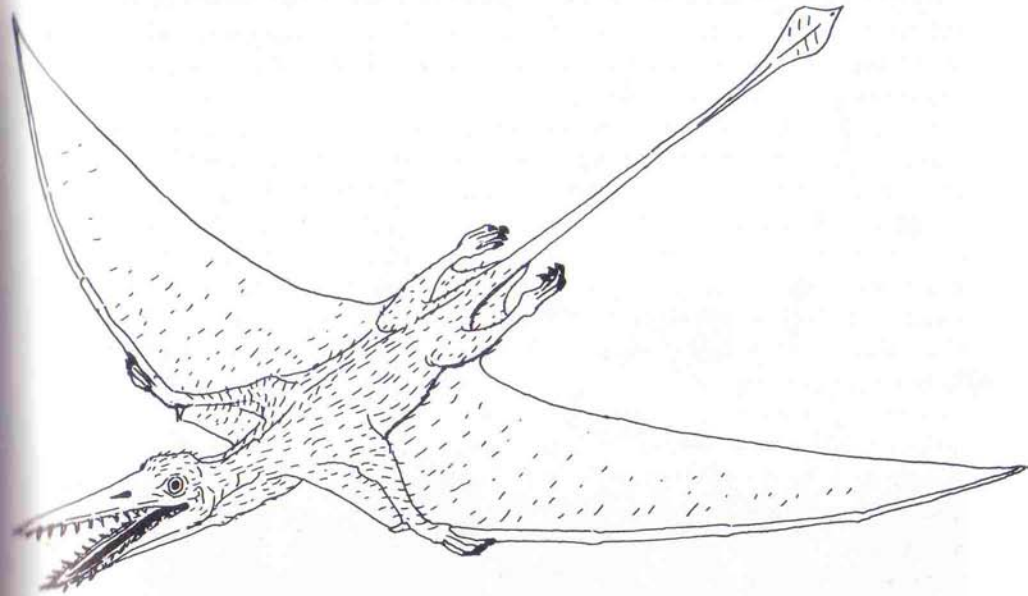
Fig. 7.86   Reconstruction of *Rhamphorhynchus*.

BIRDS

Archaeopteryx

The historical context of the discovery of *Archaeopteryx* is dealt with in chapter 1, pp. 10–15. Remarks on the mode of life are incorporated in chapter 5, pp. 84–8, and burial in chapter 6, pp. 93–6. See also figs. 7.90–7.95.

The construction of the *Archaeopteryx* skeleton is distinctly reptilian but with a few outstanding avian characteristics. About the size of a small chicken, it had long legs and a bony tail. The skull is quite primitive with the eyes still protected by bony plates and the jaws bearing teeth. *Archaeopteryx* did not have a keeled extension to its sternum, nor the fork-like terminations (uncinate processes) to the ribs which, in modern birds, serve for the attachment of flight muscles. Conversely, *Archaeopteryx* retained the abdominal ribs (gastralia) which modern birds have lost. The pelvis is typically reptilian except for the fact that the pubis probably pointed backwards. In the backbone, all the vertebrae are concave at both ends, and freely movable rather than fused. The vertebral column retained the long reptilian tail, a feature not shared with any living bird where the tail is reduced to a short bony stump but may be covered in long feathers. Three fingers on the hand are not incorporated into the wings and are freely movable as claws.
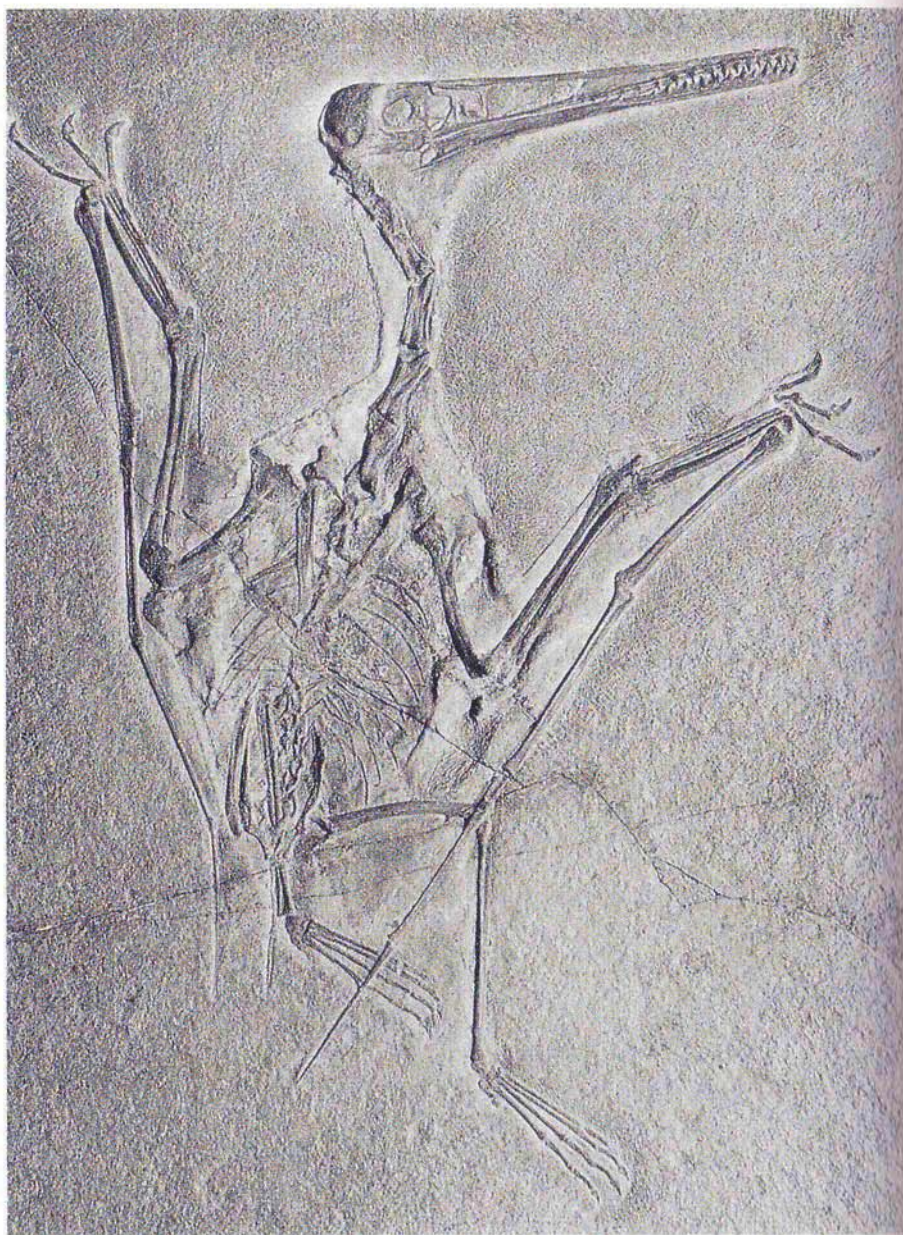
Fig. 7.87 Pterosaur; *Pterodactylus kochi* (Wagner), Eichstätt; length of skull 83 mm; BSPHGM 1937 I 18.

Fig. 7.88 Pterosaur; *Ctenochasma gracile* Oppel, Wintershof; skull length 104 mm; BSPHGM 1935 I 24.
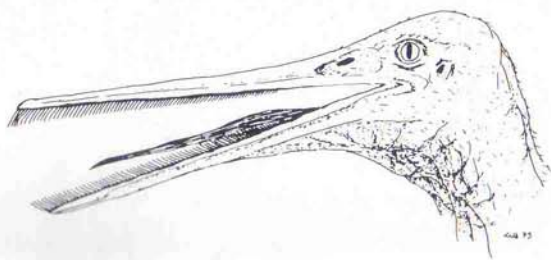
Fig. 7.89 Reconstruction of the head of *Ctenochasma*.

Haarlem specimen

Solnhofen specimen

Eichstätt specimen

Berlin specimen

London specimen

Maxberg specimen

Munich/Berlin feather

Regensburg

Kelheim

R. Altmühl

Riedenburg

Ingolstadt

R. Danube

Wokerszell

Eichstätt

Solnhofen

Dollnstein

Langen-altheim

Treuchtlingen

km

0   5   10   20

Basin deposits

Reef deposits
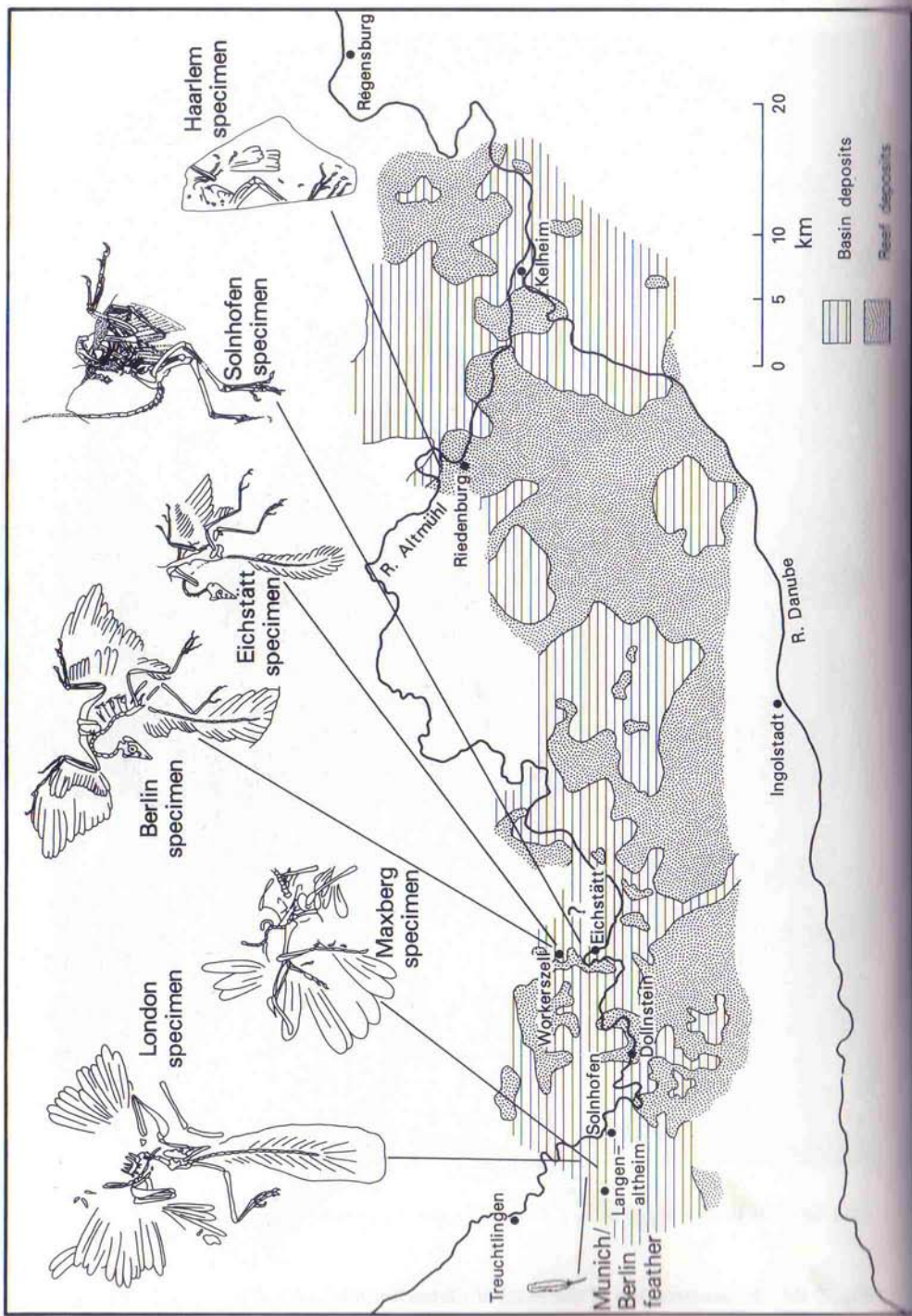
Fig. 7.92 Detail of the skull of *Archaeopteryx lithographica* Meyer; Eichstätt specimen, Workerszell bei Eichstätt; skull length 39 mm; JME.

On previous pages

Fig. 7.90 Specimens of the bird, *Archaeopteryx*, and map of their original localities. Adapted from Wellnhofer (1974, 1988b).

Fig. 7.91 *Archaeopteryx lithographica* Meyer; Eichstätt specimen, Workerszell bei Eichstätt; skull length 39 mm; JME. Copyright of that collection. Photograph by P. Wellnhofer.

However, all the *Archaeopteryx* specimens have feathers, feathers in fact so well developed that they are indistinguishable in form and distribution from the flight feathers of modern birds (discussed in greater detail on pp. 86–8). Feathers are clearly derived from reptilian scales but no reptile has feathers and it is on this one, critical feature that *Archaeopteryx* merits classification as a true bird. Several other avian characteristics have been attributed to *Archaeopteryx*. Individually each characteristic has been challenged, but the collective presence of these avian features must be more than fortuitous. One of the most commonly cited avian features of *Archaeopteryx* is the structure of the foot; the first toe opposes the other three, a feature thought to be used in perching and an exclusively avian character. Now, however, this feature has also been found in other dinosaurs. The backwardly directed pubis is also an avian feature but in *Archaeopteryx* there is debate as to whether it is original or simply due to compaction. All birds have the collar bones (clavicles) fused together into the wishbone (furcula) which prevents the chest collapsing under vigorous movement of the arms. The London specimen certainly does show a massive wishbone (which incidentally is detached and upside-down with respect to the rest of the skeleton), but a wishbone is not visible in either the Berlin or Eichstätt specimens. There have been reports that *Archaeopteryx* also had air-filled cavities in the bones, as do modern birds, but this is now no longer thought to be the case.

The six specimens of *Archaeopteryx* differ from each other in various respects, besides the obvious differences in preservation. Of the entire (or almost entire) specimens, the Eichstätt specimen differs from the other three – the Berlin, London and Solnhofen specimens. The Eichstätt specimen is about two-thirds the size of the Berlin and London specimens and half the size of the Solnhofen. Its teeth are also distinctively different (Howgate 1984a, b). They are narrow, conical and curve backwards, whilst those of the London and Berlin specimens are stouter and more peg-like. In the Eichstätt specimen the teeth interdigitated (as is probably the case also in the Berlin specimen, judging from the wear facets), whilst the London specimen had teeth which came together (occluded) when the jaw was closed. The differences must be related to a difference in diet. In addition, in the Eichstätt specimen the shoulder is poorly ossified (Wellnhofer 1974) and also differs in having longer hind limbs. It may be that the Eichstätt specimen should be a new species or even genus, or simply that it is a juvenile. Indeed, the Berlin specimen was originally assigned to a new genus but at present time the name generally used for all seven specimens (i.e. including the feather) is *Archaeopteryx lithographica* von Meyer.

Fig. 7.94 *Archaeopteryx lithographica* Meyer; Solnhofen specimen, Eichstätt area?; length from foot to restored end of tail 395 mm. Photograph by P. Wellnhofer.

Fig. 7.93 (opposite page) *Archaeopteryx lithographica* Meyer; Berlin specimen, Blumenberg bei Eichstätt; length of skull 52 mm; PAMNHUB MB 1880/81.4598, counterpart 4599.
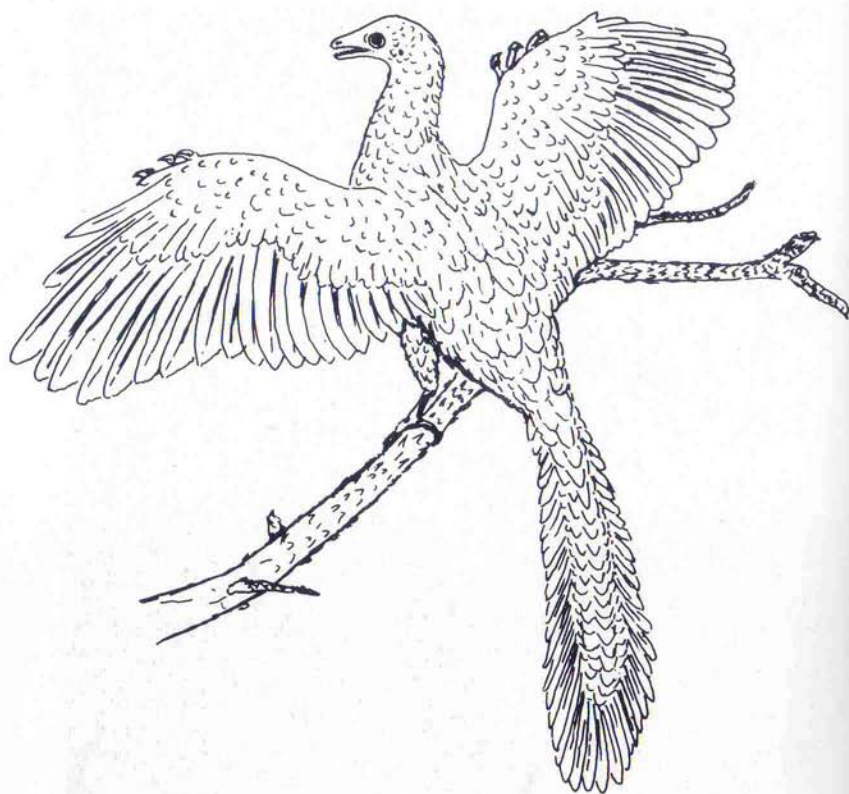
Fig. 7.95 Reconstruction of *Archaeopteryx* based on the model in the British Museum of Natural History.

Fig. 7.96   *Archaeopteryx lithographica* Meyer; the isolated feather. BSPHGM.

8 Conclusions: The Solnhofen Plattenkalk and comparisons to other plattenkalk lagerstätten

Summary of the characteristics of the Solnhofen Plattenkalk

The Solnhofen Plattenkalk contains the bodies of both marine and terrestrial organisms and must have been deposited in a shallow sea. This water was protected from ocean turbulence by an outer barrier of coral reef, and water movement was further restricted by the dead sponge–algal mounds which subdivided the Plattenkalk lagoon into smaller basins. Pulses of fine marine sediment rained down through the quiet waters to the bottom of the basins and these sediments now form the flat sheets of Plattenkalk rock. There are two lithologies: pure homogeneous limestone beds, varying in thickness from (typically) 1 to 30 cm, separated from each other by thinner beds of argillaceous limestone which range in thickness from thin laminae to beds 1–3 cm thick. Chemically, the limestone beds are almost pure calcium carbonate, with a low concentration of organic matter which gives the thickest beds a blue–grey colour when freshly broken. The limestone beds may be finely laminated on a millimetric scale, but do not usually cleave along these planes. When a limestone slab is removed from the section it shows distinct upper and lower surface textures, and the fossils occur almost exclusively on the underside of a slab.

Fossils are hard to find in the Solnhofen Plattenkalk and a day's collecting may produce nothing. Only from the established collections is it possible to compare the relative abundances of different sections of the fauna and flora although we must bear in mind that only the best preserved and most showy of specimens may be on display; poorly preserved specimens are too often discarded, even though they may be a valuable source of information. In the assemblage of marine fossils there are mainly planktonic and small nektonic organisms. Benthos is under-represented. Presumably this is because, in contrast to the inhabitants of the surface waters, they were less likely to be swept away from their normal habitats into the Plattenkalk basins. Most of the animals died as soon as they were plunged into the Plattenkalk waters so they had no opportunity to make trace fossils. The only trace fossils which are present can be attributed to species whose living relatives are particularly resistant to extremes in salinity or temperature. The best known of these is the

horse-shoe crab, *Mesolimulus*, which crawled disorientatedly in a spiral over the sediment before it succumbed to the hostile conditions. The bodies of terrestrial organisms also came to be buried in the Plattenkalk sediment. These include a large and diverse collection of flying insects as well as reptiles, such as pterosaurs and lizards, and that most celebrated bird, *Archaeopteryx*.

Other plattenkalks with exceptionally preserved fossils

Of the other plattenkalks which show special preservation, the nearest deposit to Solnhofen, both in time and space, is at Nusplingen in the adjacent Swabian Alb (e.g. Temmler 1966). This plattenkalk is slightly younger, being Kimmeridgian in age, and in a very similar geological setting. The Nusplingen plattenkalk was also laid down in a hollow between sponge–algal mounds on a broad shelf, but the sides of the Nusplingen basin were probably slightly steeper than is generally the case for the Solnhofen area. Piles of sediment regularly collapsed downslope depositing slump beds and turbidites. There are also coarse breccia beds in the sequence, which represent material eroded from the sides of the sponge mounds. Lithologically, the Nusplingen plattenkalk is different from that of Solnhofen. There is no equivalent of the thick, pure homogenous limestone beds nor of the intervening marls. The beds are equally impure (about 10% insoluble residue) and cleave on a millimetric scale along internal laminations. The Nusplingen plattenkalk also lacks the regular fine-grained constitution of the Solnhofen limestone slabs which make them suitable for lithography; there is more coarse detritus, sponge spicules and a colour banding due to varying concentrations of organic matter. The distinctive surface textures of the Solnhofen slabs are not present (perhaps, as suggested by Hückel 1970, because marly partings do not separate the limestone beds), and the fossils are not restricted to the underside of limestone slabs. However, the collection of fossils is similar in content to those from Solnhofen in so far as there are the bodies of both marine and terrestrial organisms, and in the marine collection nekton and plankton predominate. Spiral death marches are, however, not known from Nusplingen. Many of these fossils are also superbly preserved and provide further insights into Late Jurassic life.

Although frequently compared to the Solnhofen Plattenkalk, when examined closely, the plattenkalk of Sierra de Montsech (e.g. Barale *et al*. 1984) from the Mesozoic sequences on the southern flanks of the Pyrenees is lithologically quite dissimilar. Its age is Early Cretaceous (Berriasian–Valanginian), so it is younger than the Solnhofen deposit. It must have been laid down in a broadly similar, lagoon-type setting. However, this lagoon probably lay very close to the coast and, although the plattenkalk itself shows no structures indicative of emergence, other units of this sequence are inter- or

supra-tidal. There are slumps in the sequence denoting a slight slope and implying that the plattenkalk was deposited in some kind of protected basinal area. The Montsech plattenkalk is similar to the Solnhofen in that it is a finely laminated limestone but here the lithological comparison ends. Instead of a homogeneous fine-grained texture, the beds are rhythmically layered with horizons of ostracods and other bioclastic debris and pieces of torn algal mat. The plattenkalk may be quite impure, generally reddish-purple in colour and sometimes colour banded due to differences in clay, iron oxide and organic content. As at Solnhofen, the beds themselves are a few centimetres in thickness and do not cleave internally. The fossils are not located exclusively on the underside of limestone beds, but split evenly between the under- and over-lying slabs. In most respects the collection of fossils preserved in the Montsech plattenkalk is quite different from the Solnhofen assemblage. Although the fish are most numerous (including some shark eggs), in Sierra de Montsech many genera are endemic and were probably brackish water inhabitants. There are also amphibians, bird remains, many insect and some spider fossils, and large, well-preserved pieces of plants. Unlike Solnhofen most of these animals lived in the depositional basin in conditions which were probably quite equitable, and there are trace fossils including coprolites.

Another important plattenkalk outcrops in the south of France, in the southernmost parts of the French Jura mountains, near to the small village of Cerin (e.g. Enay & Hess 1970, Gall & Blot 1980). The Cerin plattenkalk, being Kimmeridgian, is roughly comparable in age to the Solnhofen and is also in a back-reef position. The Cerin beds are not dissimilar in colour or texture to those of Solnhofen. In thickness, entire beds do not reach the 30 cm achieved at Solnhofen, but the bedding on a scale of 0.5–10 cm is roughly comparable. The limestone beds are separated by fine marly partings and certainly in the lower part of the sequence there is an internal lamination. The surface of the beds is slightly undulose and some are covered by a pattern suggestive of the erosion of a thin algal mat (Gall *et al.* 1985). This feature, together with the celebrated reptile tracks which adorn some bedding planes and the predominance of small burrows in the upper part of the thicker slabs, suggest episodic sedimentation interrupted by periods of emersion (or at any rate very shallow water). Fossils are usually found on bedding planes although they do not preferentially adhere to the upper surface as is the case at Solnhofen. The assemblage is representative of a littoral environment and is dominated by fish, reefal and benthic forms being much commoner than truly pelagic varieties. Invertebrates are less common, although their coprolites and faecal pellets may be quite abundant. The terrestrial reptile fossils (rhynchocephalians, tortoises, crocodiles and pterosaurs) are also an important part of the Cerin collections.

The four examples given above – Solnhofen, Nusplingen, Sierra de Montsech and Cerin – are all plattenkalks deposited in a broadly lagoonal setting. However, plattenkalk will form in other geographical settings given the

prerequisite of a protected basin and periodic supply of lime mud. For example, there are also shallow-water deposits which are not associated with reefs, such as depressions in shelves of tectonic origin (e.g. Bear Gulch plattenkalk of Central Montana, USA; Williams 1983), or the plattenkalks of Haquel and Hjoula in Lebanon (Hückel 1970). The latter is also an example of a plattenkalk deposited under water too deep for benthic microbial/algal mats and the sediment is mostly pelagic. There are also plattenkalks which have formed in lakes, such as the Green River plattenkalks of Colorado, Wyoming and Utah (e.g. Bradley 1931, 1964). All the examples given here are plattenkalks which contain an exceptionally preserved fauna and flora. For an expanded discussion of plattenkalk deposition the reader is referred to the review article by Hemleben & Swinburne (in press).

Thus, to conclude, the Solnhofen Plattenkalk is one of the most celebrated examples of exceptional preservation in the fossil record. It is a landmark in the history of life and its classic status confers an importance and relevance to all who seek to understand the general problems of evolution. And yet it is only one of a number of plattenkalks, most of which yield some well-preserved fossils, although none approach the diversity and richness of Solnhofen. These deposits show significant features, but each also has unique characters and owes its overall nature to special combinations of geology and palaeoenvironment. The Solnhofen Plattenkalk owes much of its fossil fame to the continuing quarrying and the sharp eyes of generations of Bavarian workmen. Without *Archaeopteryx*, the celebrated death marches of doomed limulids, and the exquisitely preserved flying reptiles and fish, palaeontology and evolutionary biology would be much impoverished. The Solnhofen Plattenkalk is a unique deposit, but it is evident that a greater investment into systematic and scientific excavations of plattenkalks (and other types of lagerstätte) will open new vistas into the vanished worlds of the past.

Appendix
Faunal and floral list

The macrofossil list is derived directly from Barthel's book with only minor corrections and additions, and so many names may already be out of date. The microfossils come from two additional sources: the entire list of foraminifera from Groiss (1967) and the calcareous nannoplankton from Keupp (1977).

Monerans

Cyanobacteria

Protists

Coccolithophorids
Bidiscus bellis (Noel)
Bidiscus ignotus (Gorka)
Biscutum ellipticum (Gorka)
Cyclagelosphaera margereli Noel
Ellipsagelosphaera britannica (Strandner)
Ellipsagelosphaera keftalrempti Grün
Ellipsagelosphaera ovata (Bukry)
Microstaurus alcmonensis Keupp
Podorhabdus cylindratus Noel
Podorhabdus dietzmanni (Reinhardt)
Staurorhabdus quadriarcullus (Noel)
Stephanolithion bigoti Deflandre
Watznaueria barnesae (Black)
Watznaueria deflandrei (Noel)
Zeugrhabdotus noeli Rood, Hay & Barnard
Zeugrhabdotus salillum (Noel)
?Loxolithus sp.
?Tetralithus pyramidus Gardet

Calcareous nannoplankton of uncertain systematic position
>*Pseudolithraphidites multibacillatus* Keupp
>*Pseudolithraphidites quattuorbacillatus* Keupp

Calcispheres
>*Pithonella gustafsoni* Bolli
>*Pithonella* cf. *thayeri* Bolli
>*Pithonella piriformis* Keupp

Foraminiferans
>*Gaudryina bukowiensis* Cushman & Glazewski
>*Marginulina distorta* Kusnetzowa
>*Nodosaria euglypha* Schwager
>*Patellina feifeli* (Paalzow)
>*Quinqueloculina egmontensis* Lloyd

Radiolaria indet.

Plants

Non-vascular plants

Phaeophytes, brown algae
>*Phyllothallus*

Vascular plants

Gymnosperms
>Pteridosperms
>>*Cycadopteris*
>Bennettitales
>>*Sphenozamites*
>>*Zamites*
>Ginkgos
>>*Baiera* (sometimes known as *Furcifolium*)
>>*Ginkgo*
>Conifers
>>*Araucaria*
>>*Arthrotaxites* (prev. *Echinostrobus*)
>>*Brachyphyllum*
>>*Palaeocyparis*

Animals

Invertebrates
Sponges
Ammonella
Tremadictyon

Cnidarians
Scyphozoans, jellyfish
Cannostomites
Epiphyllina
Eulithota
Leptobrachites
Quadrimedusina
Rhizostomites (includes *Myogramma, Hexarhizites &*
Ephyropsites)
Semaeostomites
Hydrozoans
Acalepha
Acraspedites
Hydrocraspedota
Anthozoans, corals
'Iridogorgonia'

Annelids
Ctenoscolex
Eunicites
Serpula

Bryozoans

Brachiopods
Lacunosella
Loboidothyris
Septaliphoria

Molluscs
Bivalves
Arcomytilus
Buchia (prev. *Aucella*)
Eopecten

   Inoceramus
   Liostrea
   Pinna
   Solemya
  Gastropods
   Ditremaria
   Globularia
   'Patella'
   Rissoa
   Spinigera
  Cephalopods
   Squids & cuttlefish
    Acanthoteuthis
    Celaenoteuthis
    Geopeltis
    Kelaeno
    Leptoteuthis
    Palaeololigo
    Plesioteuthis
    Trachyteuthis
see also Engeser & Reitner (1981) & Engeser (1986)
   Belemnites
    Duvalia
    Hibolites
    Raphibelus (possibly a juvenile of *Duvalia*)
   Nautiloids
    Pseudaganides
   Ammonites
    Aspidoceras
    Glochiceras lithographicum (Oppel)
    Glochiceras solenoides (Quenstedt)
    Gravesia
    Hybonoticeras hybonotum (Oppel)
    Lithacoceras
    Neochetoceras steraspis (Oppel)
    Subplanites
    Sutneria
    Taramelliceras prolithographicum (Fontannes)

Arthropods

Crustaceans
Malacostracans
  Mysidaceans
      Elder
      Francocaris
  Isopods
      Palaega
      Urda
  Decapods
    Natantians
        Acanthochirana
        Aeger
        Antrimpos
        Blaculla
        Bombur
        Bylgia
        Drobna
        Dusa
        Hefriga
        Rauna
        Udora
        Udorella
    Reptantians
        Cancrinos
        Cycleryon
        Eryma
        Eryon
        Etallonia
        Glyphaea
        Knebelia
        Magila
        Mecochirus
        Nodoprosopon
        Palaeopentacheles
        Palaeopolycheles
        Palinurina (and juvenile prev. *Phyllosoma*)
        Pseudastacus
        Stenochirus
    Stomatopods
        Sculda

Crustaceans of unknown affinity
>*Anthonema* (juvenile crustacean)
>*Palpipes* (juvenile crustacean)

Ostracods

Cirripedes, barnacles
>*Archaeolepas*
>*Brachyzapfes* (trace fossil)

Chelicerates

Xiphosurans
>*Mesolimulus*

Arachnids
>*Sternarthron*

Insects

Ephemopterans, mayflies
>*Hexagenites*

Odonatans, dragonflies
>*Aeschnidium*
>*Aeschnogomphus*
>*Anisophlebia*
>*Euphaeopsis*
>*Isophlebia*
>*Libellulium* (prev. *Cymatophlebia*)
>*Nannogomphus*
>*Protolindenia*
>*Pseudoeuphaea*
>*Steleopteron*
>*Stenophlebia*
>*Tarsophlebia*
>*Urogomphus*

Blattoideans, cockroaches
>*Lithoblatta*
>*Megalocerca*
>*Progeotrupes*

Phasmidans, water skaters
>*Chresmoda*

Ensiferans, locusts & crickets
>*'Elcana'*
>*Jurassobatea*
>*Pycnophlebia*

Heteropterans, bugs & water scorpions
    Mesobelostomum
    Mesocorixa
    Mesonepa
    Notonectites
    Sphaerodemopsis

'Auchenorryhnchans', cicadas
    Archepsyche
    Eocicada
    Limacodites
    Protopsyche

Neuropterans, lacewings
    Archegetes
    Kalligramma
    Mesochrysopa
    Osmylites

Coleopterans, beetles
    Actaea
    Amarodes
    Apiaria
    Cerambycinus
    Curculionites
    Eurthyreites
    Hydrophilus
    Malmelater
    Notocupes
    Omma
    Oryctites
    Procalosoma
    Pseudohydrophilus
    Pseudothyrea

Hymenopterans, bees & wasps
    Pseudosirex

Trichopterans, caddis flies
    Archotaulius
    Mesotaulius

Dipterans, flies
    Empidia
    Prohirmoneura

see updated review in Ponomarenko (1985)

Echinoderms

Crinoids, sea-lilies
>*Millericrinus*
>*Pterocoma* (prev. *Antedon*)
>*Saccocoma*
>*Solanocrinites*

Asteroids, starfish
>*Lithaster*
>*Pentasteria*

see also Hess (1986)

Ophiuroids, brittle stars
>*Geocoma*
>*Ophiopsammus* (prev. *Ophiocten*)
>*Ophiurella*

Echinoids, sea-urchins
>*Collyropsis*
>*Hemicidaris*
>*Pedina*
>*Phymopedina*
>*Plegiocidaris*
>*Pseudodiadema*
>*Rhabdocidaris*
>*Tetragramma*

Holothurians, sea-cucumbers
>*Achistrum*
>*Eocaudina*
>*Hemisphaeranthos*
>*Priscopedatus*
>*Protoholothuria*
>*Pseudocaudina*
>*Theelia*

Trace fossils

>*Lumbricaria intestinum*
>*Lumbricaria recta*

Vertebrates

Fish

Chondrichthyes
Selachians, sharks
Galeus (prev. *Pristiurus*)
Heterodontus (prev. *Paracestracion*)
Hexanchus (prev. *Notidanus*)
Hybodus
Orectolobus (prev. *Palaeocrossorhinus* & *Crossorhinus*)
Palaeocarcharias
Palaeoscyllium
Phorcynis
Protospinax (=*Belemnobatis*)
Pseudorhina (prev. *Squatina*)

Batoideans, rays
Aellopos (prev. *Spathobatis*)
Asterodermus

Chimaeriforms, ratfish
Chimaeropsis
Ischyodus

Osteichthyes, bony fish

Actinopterygii, ray-finned fish
Chondrosteans, cartilaginous ganoid fish
Coccolepis

Holosteans, bony ganoid fish
Semionotiformes
Heterostrophus
Lepidotes

Pycnodontiformes
Eomesodon
Gyrodus
Gyronchus (prev. *Mesodon*)
Mesturus
Proscinetes (prev. *Microdon*)

Amiiformes
Asthenocormus
Callopterus
Caturus
Caturus (*Strobilodus*)

       Eurycormus
       Eusemius
       Furo (prev. *Eugnathus* & *Isopholis*)
       Histionotus
       Hypsocormus
       Ionoscopus
       Liodesmus
       Macrosemius
       Notagogus
       Ophiopsis
       Orthocormus
       Propterus
       Sauropsis
       Urocles (prev. *Megalurus*)

    Aspidorhynchiformes
       Aspidorhynchus
       Belonostomus

    Pholidophoriformes
       Oligopleurus
       Pholidophorus
       Pleuropholis

    Teleosts, modern bony fish
       Allothrissops
       Anaethalion
       Ascalabos
       Leptolepides
       Orthogonikleithrus
       Pachythrissops
       Tharsis
       Thrissops
see also Nybelin (1974) & Arratia (1988)

    Crossopterygii, lobe-finned fish
       Coccoderma
       Holophagus (prev. *Undina*)
       Libys

Reptiles

    Chelonians, turtles
       Eurysternum
       Idiochelys
       Platychelys
       Plesiochelys

Ichythyosaurs
    Leptopterygius
    Macropterygius

Plesiosaurs
    Stretosaurus (one tooth)

Lacertilians, lizards
    Ardeosaurus
    Bavarisaurus
    Eichstaettisaurus
    Palaeolacerta
    Proaigialosaurus

Rhynchocephalians
    Acrosaurus
    Homeosaurus
    Kallimodon
    Piocormus
    Pleurosaurus

Crocodiles
    Aeolodon
    Alligatorellus
    Alligatorium
    Atoposaurus
    Dacosaurus
    Geosaurus
    Steneosaurus

Saurischian dinosaurs
    Compsognathus

Pterosaurs
    Anurognathus
    Ctenochasma
    Germanodactylus
    Gnathosaurus
    Pterodactylus
    Rhamphorhynchus
    Scaphognathus

Birds

    Archaeopteryx

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Systematic index

This index lists both scientific and common names used in the book down to genus level. The main descriptions of the fossils will be found in the page references between 102 and 201 (i.e. Chapter 7); the rest of the page references deal with other aspects of the fossils' occurrences, way of life, preservation, etc. The Appendix (faunal and floral list) is not indexed. Illustrations are indicated by italic page numbers; both the genera and larger groups are indexed for the figures not in Chapter 7, while those in Chapter 7 are just indexed by the genus.

Systematic index

General index

This index includes all subjects other than systematic names, which are covered in a separate index. Place names from individual figures of the fossils are not indexed, but references are given to some of the figures in the first six chapters of the book where it is felt they may be useful (e.g. to general views of quarries).

The celebrated Solnhofen Limestone is among the most important fossil deposits because of its astonishing diversity of organisms, many exquisitely preserved. Marine and terrestrial creatures and plants, buried 150 million years ago in soft lagoonal muds, provide a unique glimpse into the true diversity of Jurassic life. Articulated skeletons are preserved, as well as some soft-bodied animals that otherwise would be too delicate to survive fossilisation. Among the highlights are superbly preserved jellyfish, crustaceans, squid, fish and flying reptiles. Perhaps most important of all is *Archaeopteryx* – the celebrated 'missing link' which has the skeleton of a dinosaur but is covered in feathers, revealing a crucial evolutionary transition between the reptiles and birds. Solnhofen opens a window into a vanished world, and reveals the unexpected richness of a land and sea teeming with life.

This book is a revised and updated translation of Werner Barthel's classic work *Solnhofen: Ein Blick in die Erdgeschichte*. In revising the text, Nicola Swinburne and Simon Conway Morris have added a considerable amount of new material whilst preserving the spirit of the original book. This is an authoritative account of the geological history, palaeoecology, palaeoenvironment and fossil taxonomy of this classic location. Not only will it be of great interest to palaeontologists and evolutionary biologists, but it will also be of value to amateur collectors, natural historians and also those with an interest in the history of life.

'This book is an excellent testament to one of the most famous limestones in the geologic record.' *American Scientist*

'Geologists are now indebted to Nicola Swinburne and Simon Conway Morris for an excellent general survey . . . of the considerable body of research by German sedimentologists and taphonomists during the last 25 years'. *Nature*

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